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STUDIES ON NEW VARIETIES OF APPLE ROOTSTOCKS

By H. M. TYDEMAN
East Malling Research Station

It is now almost twenty years since a joint programme of breeding and testing new varieties of apple rootstocks was arranged between the East Malling Research Station and the John Innes Horticultural Institution. Hatton (1, 2, 3, 4) had already made considerable progress in his studies of the influence of the sixteen varieties of so-called "Paradise" rootstocks, collected at East Malling, upon apple scions, and was in a position to forecast something of the limitations as well as the potentialities of this series. The early interest in the genetics of fruit trees of Prof. Bateson and his assistant, Mr. M. B. Crane, made possible the joint arrangement whereby the facilities for plant breeding work, available at the John Innes Horticultural Institution, could be used for making crosses between the various rootstocks, the seedlings from which were sent to East Malling later to be tested as possible rootstocks. Thus, while the specialist knowledge of plant breeding methods possessed by Mr. Crane could be utilized in raising the families of seedlings, their testing could be undertaken at East Malling, where experience in comparing the different races of rootstocks had been accumulating.

Almost from the beginning, work was directed towards two somewhat dissimilar objects. On the one hand, a large number of crosses were made between certain Malling selected "Paradise" rootstocks and varieties like Northern Spy, which were reputed to be immune from attack by Woolly Aphis. It was hoped that new races of rootstocks would be originated, combining the wide range of influence over the scion and ease of multiplication possessed by certain members of the "Paradise" series, with immunity from attack by Woolly Aphis. A considerable literature dealing with this work now exists (5, 6, 7, 8).

From 1917 onwards, crosses were made between various Malling selections of "Paradise" rootstocks. From the economic point of view, crosses were directed towards the combination in single seedlings of complexes of characters borne separately in the existing varieties of rootstocks, or the origination of new characters of value. At the same time it was hoped that such crosses would yield information of genetic interest.

The present paper deals with seedlings from a cross, made in 1923, by Crane, between the French Paradise (Malling No. VIII) and Jaune de Metz (Malling No. IX). The two rootstocks stand quite apart from the rest of the

Malling series of "Paradise" because of their relatively extreme dwarfing effect on the scion. This is strikingly associated with "precocity", that is, the capacity to bear prolific quantities of blossom and comparatively heavy crops of fruit relatively early in the life of the tree. Although they exert an almost identical influence on the scion, Malling No. IX has almost completely superseded Malling No. VIII in commerce as the typical "dwarfing" rootstock, because the latter is very susceptible to apple Scab and Mildew. Crane's principal object in making the cross was to study the inheritance of the dwarfing character in the unworked seedlings. They were sent to East Malling in 1926, because it was thought that they might include valuable new dwarfing and semi-dwarfing rootstocks.

The Trials.

Altogether 136 seedlings from this cross were tested to ascertain the ease with which they could be vegetatively propagated. Ultimately, nineteen were selected as showing good promise. These were then multiplied in sufficient quantities for budding in order to obtain information as to their influence upon the scion. The scion used throughout was Lane's Prince Albert, because it was already known to be a quick indicator of differential rootstock effects. Three trials were laid out as follows:—

Trial A. Comprising ten rootstocks, budded in 1930. There was a unit of between fifteen and thirty-five trees on each rootstock and forty-five trees on Malling No. IX.

Trial B. Containing fifty trees on each of nine rootstocks, budded in 1932, with control trees on Malling Nos. IX and VII. Trees on No. VII were included because it was hoped to find among the seedlings, rootstocks combining the early vigour and precocity characteristic of this variety, but without its faults.

Trial C. A unit of forty trees on each of the nineteen rootstocks was budded in 1933 for a complete trial. Trees on Malling Nos. IX and VII were again included. The results of this trial will be discussed most fully, but those from the preliminary Trials A and B have been included because they are to a large extent confirmatory.

The Method of the Intensive Trial.

Since it was desired to test a considerable number of these new rootstocks, it was decided to devise a special method for testing them on an intensive scale. They were planted out in nursery rows at 5 to 6 feet apart, the rootstocks being from 2 to 2½ feet apart in the rows, and were budded in situ. Latterly, it has been usual to insert more than one bud into each rootstock in

order to eliminate bud failures, with the consequent disturbing effect on the experiment of gaps in the rows. The trees were allowed to grow where they were budded, being left unpruned or only lightly regulated. They were trained to canes and wires in their early years and, where they showed signs of becoming crowded at the end of a few years, alternate trees were removed without disturbing the roots of adjacent trees. This process of removing alternate trees was repeated at intervals until, at the end of six years, the trees in the oldest of these trials were spaced at intervals of eight or ten feet.

For this intensive type of trial it was necessary to have a comparatively large unit of trees. Thus, in the 1932 trial, there was a unit of fifty trees on each rootstock and, in the complete trial budded in 1933, units of forty trees. In both trials the trees were planted in blocks of ten and randomized in five, and in four, different positions on the plantation respectively.

THE RECORDS.

The observations and records made on these trees were designed to provide information as to the influence of the rootstock on (1) the vigour, (2) the productivity, and (3) the health of the scion.

I. THE INFLUENCE OF THE ROOTSTOCK ON THE VIGOUR OF THE SCION.

(a) AS MEASURED BY THE LENGTH OF NEW WOOD.

The length of new wood was measured each winter, and the records are summarized in Table I. The most notable feature is the extremely wide range of variation in the vigour which these rootstocks have imparted to the scion. Thus, in Trial C, during three seasons, while the trees on No. 70 had made only 718 cm. of new wood, those on No. 89 had made 3,127 cm. The trees on the remaining seventeen rootstocks ranged themselves between these two extremes. The variation, however, does not appear to be strictly continuous. This is shown well in Diagram A.

Thus, trees on the first three rootstocks are separated by a considerable interval from the next five which, in turn, are considerably less vigorous than the next three, which include the sets of trees on Malling No. IX. Trees on Nos. 116 and 90 are, in turn, considerably less vigorous than the trees on the remaining seven rootstocks. It was possible, on the basis of these differences, to separate the rootstocks into five groups. This grouping is confirmed by a statistical analysis of the totals of new wood for 1936 of the trees in Trial C, and although there are some exceptions, is supported by the records of the trees in Trials A

and B. At the same time it should be pointed out that this result may possibly have been due to the comparatively small number of rootstocks studied and that had the numbers been larger, the variation might have been found to have been continuous. The extreme differences in vigour are well illustrated in Figs. 1 and 2.

Since units of trees on Malling No. IX were planted for comparison in all three of these trials, and trees on Malling No. VII were planted in the two more recent trials, B and C, it is possible to make a direct comparison between the trees on the VIII × IX rootstocks and those on the two varieties of

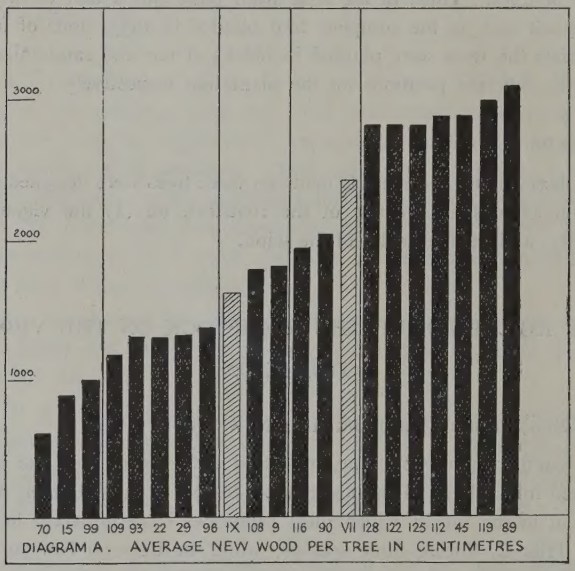

DIAGRAM A. AVERAGE NEW WOOD PER TREE IN CENTIMETRES

"Paradise". Table I shows that trees on eight of these rootstocks, in the complete Trial C, had made less wood during their first three years than had those on Malling No. IX, the least vigorous of the Malling series, while eleven of them had made a significantly greater amount of new wood. The two older trials do not contain the complete range of rootstocks, and it is less easy to assign a definite position to the trees on Malling No. IX. In Trial A, the trees on three of the rootstocks had made a smaller aggregate of new wood, on the average, by the end of their sixth year, than had those on Malling No. IX; and those on seven rootstocks had made a greater amount, although trees on two of them, Nos. 93 and 22, had been assigned to a less vigorous group on the basis of the new wood totals of younger trees. The trees in Trial B have

TABLE I.

Average New Wood per Tree in Centimetres.

Rootstock No.	Trial A. Budded in 1930. Six years total.	Trial B. Budded in 1932. Four years total.	Trial C. Budded in 1933. Three years total.
Group 1.			
70	—	—	718
15	—	—	896
99	—	403	997
Average :	—	**403**	**871**
Group 2.			
109	1,873	—	1,155
93	2,670	—	1,330
22	2,954	—	1,332
29	1,771	503	1,350
96	—	—	1,395
Average :	**2,324**	**503**	**1,313**
Group 3.			
IX	2,239	458	1,644
108	3,176	530	1,801
9	2,107	359	1,833
Average :	**2,508**	**449**	**1,760**
Group 4.			
116	—	—	1,957
90	—	785	2,025
VII	—	541	2,462
Average :	—	**664**	**2,148**
Group 5.			
128	—	774	2,838
122	—	—	2,844
125	9,818	951	2,855
112	6,902	1,060	2,937
45	5,624	1,134	2,966
119	—	—	3,057
89	8,006	—	3,127
Average :	**7,588**	**980**	**2,946**

made very unsatisfactory growth throughout and, by the end of their fourth year, those on Malling No. IX had actually made little more than a quarter of the new wood made in three years by the trees on Malling No. IX in Trial C. In spite of this, the trees on the rootstocks represented in Trial B had, with few exceptions, ranged themselves in the same relative order as the trees on the same rootstocks in Trial C. As was expected, the trees on Malling No. VII made considerably more new wood than those on Malling No. IX. It is noteworthy, therefore, that, in Trial C, trees on seven of the selections from

VIII x IX had made, on the average, a greater amount of new wood by the end of their third year.

Although it is impossible to make any direct comparison of the relative vigour of the trees on the VIII x IX seedlings and those on the sixteen varieties of "Paradise" included in Hatton's original trials, since neither cultural nor seasonal conditions were similar, there are grounds for supposing that the more vigorous rootstocks in both series were about equally vigorous by the end of their third year. Trees of Lane's on the dwarfing Malling No. IX, in

TABLE II.

Diameter of Stem in Centimetres. Average per Tree.

Rootstock No.	Trial A. Budded in 1930. At six years old.	Trial B. Budded in 1932. At four years old.	Trial C. Budded in 1933. At three years old.
Group 1.			
70	—	—	1·73
15	—	—	1·97
99	—	1·51	1·74
Average :	—	**1·51**	**1·81**
Group 2.			
109	3·02	—	2·23
93	3·64	—	2·29
22	3·61	—	2·49
29	3·14	1·66	2·16
96	—	—	2·18
Average :	**3·36**	**1·66**	**2·27**
Group 3.			
IX	3·23	1·74	2·47
108	3·94	1·79	2·48
9	3·05	1·63	2·33
Average :	**3·41**	**1·72**	**2·42**
Group 4.			
116	—	—	2·80
90	—	2·05	2·74
VII	—	1·98	3·12
Average :	—	**2·01**	**2·89**
Group 5			
128	—	2·36	3·37
122	—	—	3·33
125	6·58	2·52	3·35
112	5·83	2·45	3·29
45	5·51	2·46	3·51
119	—	—	3·58
89	6·03	—	3·49
Average :	**5·98**	**2·45**	**3·42**

Hatton's trial,* made 49% of the wood made by the trees on the very vigorous Malling No. XII ; trees on No. IX in this trial made 52% of the wood made by the trees on No. 89, the most vigorous of these seedlings. Again, trees on the semi-dwarfing Malling No. VII, in Hatton's trial, made 84% of the wood made by those on No. XII, while, in this trial, trees on No. VII made 79% of the wood made by trees on No. 89. By the end of their sixth year, the similarity is less close. Trees on No. IX in Hatton's trial, made 20% of the wood made by those on No. XII, but, on No. IX, in this trial the trees made 28% of the wood made by those on No. 89. The results of such comparisons should, however, be received with the greatest caution since the very different conditions under which the two trials were carried out may have had a greater effect on certain rootstocks than on others, which would have affected their relative positions within the series.

(b) As Measured by Diameter of Stem.

The records include measurements of the thickness of the stem at a uniform height above the union. They are summarized in Table II.

The rootstocks are arranged in ascending order of vigour as expressed by new wood. In general, stem diameter appears to have been an equally efficient measure of the relative vigour of these trees. Table II shows that while there are minor alterations in the relative positions of the rootstocks within the groups, only Groups 2 and 3 overlap. Thus, the trees on No. 22, in Group 2, Trial C, were slightly stouter, on the average, than those on any of the rootstocks in Group 3, while at six years old, in Trial A, the trees on Nos. 93 and 22 were stouter than those on the two rootstocks Malling No. IX and No. 9, in Group 3. In Trial C the trees on Malling Nos. IX and VII retained their relative positions in Group 3 and 4 respectively. With slight exceptions, there appears to have been a very close correlation between new wood and stem thickness throughout.

(c) As Measured by Weight of Tree.

The weight of the tree is, perhaps, the most complete expression of tree size obtainable. The periodical thinning out of the trees in these trials has made it possible to record the weight of the trunk and branches at various ages. In Table III are summarized the trunk and branch weights of from seven to fifteen trees on each rootstock, removed at five years old from Trial A, and of thirty trees on each rootstock, in Trial B, removed at four years old. In the

* See R. G. Hatton, "The Influence of Different Rootstocks upon the Vigour and Productivity of the Variety Budded or Grafted Thereon." Journ. Pom. & Hort. Sci., 1927, 6, Appendix A.

TABLE III.

Weight of Tree at Removal.

Rootstock No.	Trial A. Removed at five years old in lbs.	Trial B. Removed at four years old in lbs.
Group 1.		
99	—	1·18
Average :	—	**1·18**
Group 2.		
109	2·16	—
93	2·51	—
22	3·26	—
29	2·05	1·25
Average :	**2·50**	**1·25**
Group 3.		
IX	2·56	1·41
108	2·46	1·67
9	3·00	1·04
Average :	**2·68**	**1·37**
Group 4.		
90	—	2·06
VII	—	1·79
Average :	—	**1·93**
Group 5.		
125	5·46	2·38
112	5·80	2·50
45	5·11	2·54
89	5·40	—
128	—	2·27
Average :	**5·44**	**2·42**

latter, the weights are of entire trees, including the root systems. These figures provide an almost perfect confirmation of the data on tree size already given. In Trial A, in spite of slight overlapping between the trees on the rootstocks in Groups 2 and 3, vigour of tree as expressed by weight shows very close correspondence with vigour as expressed by new wood and diameter of stem. In Trial B, the only anomalous case is that of trees on seedling No. 9, in Group 3, which were lighter, on the average, than those on No. 29, in Group 2, or No. 99, in Group 1. Since, however, the trees on this rootstock had made less new wood by the end of their fourth year than the trees on the other two rootstocks, this result was only to have been expected.

It is a little remarkable that a cross between two such rootstocks as Malling Nos. VIII and IX, which have been shown to induce so pronounced

a dwarfing effect on apple scions, should have given rise to seedlings showing so wide a range of variation in their influence upon the vigour of Lane's Prince Albert, at least during the early years. At one extreme, eight rootstocks have made trees less vigorous than those on Malling No. IX, up to the end of their third year ; indeed, trees on the most dwarfing of them, No. 70, had made less than half the wood growth made by those on No. IX. At the other, seven rootstocks were definitely more vigorous than Malling No. VII, a fairly vigorous rootstock during its early years. This result appears to provide another illustration of the extremely heterozygous condition of apple varieties ; it also proves that potentialities for vigour must exist in such dwarfing rootstocks as Malling Nos. VIII and IX, probably due to complementary factors borne separately by the two varieties, which can come together only when they are crossed.

TABLE IV.

Illustrating the Relation between the Size of the Swelling at the Union and the Average Size of the Tree.

Rootstock No.	Diameter at Union in cm.	Diameter at 3 in. above Union in cm.	Percentage Increase.
Group 1.			
99	4·10	1·67	145·6
Average :	**4·10**	**1·67**	**145·6**
Group 2.			
29	4·37	1·86	136·2
Average :	**4·37**	**1·86**	**136·2**
Group 3.			
IX	4·62	1·93	139·8
108	3·93	1·98	100·2
9	3·55	1·62	143·2
Average :	**4·03**	**1·84**	**127·7**
Group 4.			
90	4·94	2·30	116·6
VII	3·11	1·91	63·2
Average :	**4·03**	**2·11**	**89·9**
Group 5.			
128	3·77	2·34	61·6
125	3·91	2·59	50·5
112	4·72	2·75	71·8
45	4·16	2·72	53·7
Average :	**4·14**	**2·60**	**59·4**

(d) The Relation between Size of Tree and the Swelling at the Union.

A noticeable characteristic of the trees on many of the types of "Paradise" rootstocks is the presence of a large swelling at the point of union. This is particularly pronounced on trees on the dwarfing rootstocks Nos. VIII and IX and on No. IV, a vigorous rootstock in its early years. This swelling increases in size more rapidly than the rest of the tree and, in extreme cases, may prove very unsightly. Such swellings were very common on the trees on certain of the rootstocks of the VIII × IX series. Since they appeared to occur more

Table V.

Average Number of Blossom Trusses per Tree.

Rootstock No.	Trial A. Budded in 1930. Six years total.	Trial B. Budded in 1932. Four years total.	Trial C. Budded in 1933. Three years total.
Group 1.			
70	—	—	76·7
15	—	—	72·0
99	—	81·8	78·3
Average :	—	**81·8**	**75·7**
Group 2.			
109	340·3	—	64·0
93	421·3	—	71·7
22	387·0	—	69·9
29	395·1	75·0	89·3
96	—	—	77·6
Average :	**385·9**	**75·0**	**74·5**
Group 3.			
IX	421·1	81·9	81·3
108	500·8	98·9	78·6
9	433·1	70·6	69·0
Average :	**451·7**	**83·8**	**76·3**
Group 4.			
116	—	—	66·0
90	—	97·7	57·2
VII	—	90·9	40·7
Average :	—	**94·4**	**54·7**
Group 5.			
128	—	85·1	46·2
122	—	—	53·5
125	830·0	88·9	39·2
112	707·3	102·9	47·7
45	606·0	97·5	62·0
119	—	—	49·1
89	566·3	—	51·3
Average :	**680·2**	**93·6**	**49·8**

commonly on trees growing on the less vigorous rootstocks, it was thought probable that the size of the swelling was closely associated with tree size. Measurements of the sizes of the swellings on nine of these rootstocks were made when the trees were four years old. The diameters of the stems at the point of union and at three inches above were measured. The percentage difference between the diameters at these two points was taken as the measure of the relative size of the swelling. The average figures for units of ten trees on each rootstock are shown in Table IV. The rootstocks are arranged in order of increasing vigour as measured by new wood. With only slight exceptions, the size of the swelling decreases with the increasing size of the tree. Although there were minor variations, in general, the size of the swelling was found to be very constant from tree to tree on the same rootstock.

II. THE INFLUENCE OF THE ROOTSTOCK ON THE PRODUCTIVITY OF THE SCION.

(a) As Measured by Blossom Production.

While it will be obvious that the ultimate criterion of the relative productiveness of fruit trees must lie in a comparison of the crops of fruit which they are capable of carrying, the incidence of adverse weather conditions, premature dropping and the depredations of insect pests, may seriously impair the value of such records. It has always been thought advisable, therefore, to supplement the data on actual fruit production, with counts of the blossoms borne.

The number of trusses were counted each year. The records are summarized in Table V. They show that, at least up to the end of their third year, blossom production was closely associated with the dwarfing character in the trees on these rootstocks. Although the trees on No. 29, in Group 2 (Trial C), had actually produced a larger number of trusses than had those on any other rootstock in the series, and the trees on No. 108 in Group 3 had borne a larger number than had the trees on any of the rootstocks in Group 1, a fairly consistent reduction in the average number of trusses occurs between the trees on the least vigorous and those on the more vigorous rootstocks. This tendency becomes very marked among the more vigorous rootstocks in Groups 4 and 5. At the end of six years, however, this result had been completely reversed and the trees on the four vigorous rootstocks represented (Group 5 in Trial A), had produced about twice as many trusses as had those on the four dwarfing rootstocks in Group 2. This result had unquestionably been brought about at least in part by the greatly increased size, and consequently greater blossom bearing surface, of the trees on the vigorous rootstocks.

(b) The Relation between Blossom Formation and Tree Size.

While the foregoing data illustrate very clearly the differences found in the actual number of trusses, since the trees differed widely in size, it is clear that the figures in Table V do not provide an adequate picture of the relative precocity of the trees. Thus, the much greater number of trusses borne by the trees on the vigorous rootstocks, at six years old, when compared with the trees on the more dwarfing rootstocks, may have been entirely due to their much greater size, or may indicate that the trees on the more vigorous

Table VI.

Average Number of Blossom Trusses per 100 centimetres of New Wood.

Rootstock No.	Trial A. Budded in 1930. Six years average.	Trial B. Budded in 1932. Four years average.	Trial C. Budded in 1933. Three years average.
Group 1.			
70	—	—	16
15	—	—	12
99	—	26	14
Average :	—	**26**	**14**
Group 2.			
109	20	—	12
93	18	—	10
22	15	—	11
29	24	19	12
96	—	—	13
Average :	**20**	**19**	**12**
Group 3.			
IX	20	21	9
108	16	22	9
9	33	26	7
Average :	**23**	**23**	**8**
Group 4.			
116	—	—	7
90	—	14	6
VII	—	18	3
Average :	—	**16**	**5**
Group 5.			
128	—	12	3
122	—	—	3
125	9	12	3
112	10	12	3
45	12	10	3
119	—	—	3
89	8	—	4
Average :	**10**	**12**	**3**

rootstocks were entering on a definitely more productive stage by their sixth year. In order to make possible a comparison of the actual productiveness of the trees on the different rootstocks, irrespective of their size, the average number of trusses borne per hundred centimetres of new wood made have been calculated and the results for the three trials are shown in Table VI. When treated in this way the six year old trees show a decrease in productiveness with the increasing vigour of the rootstocks similar to that shown by the trees at an earlier age. Thus, the trees on No. 29 in Group 2 bore an average of twenty-four blossom trusses per 100 centimetres of new wood, while those on No. 89 in Group 5 bore only eight. The Table illustrates very clearly the much greater productiveness of the trees on the rootstocks in the extra dwarf groups, 1 and 2, when compared with those in the third and subsequent groups.

These figures lend some support to the view that, with advancing age, the trees on the more vigorous rootstocks were becoming increasingly productive as compared with those on the more dwarfing rootstocks. Thus, if minor variations are excluded, the five rootstocks in Group 2 (Trial C) bore, on the average at three years old, just four times as many trusses per centimetre of wood as did the seven rootstocks in Group 5 (Trial C) ; but, at six years old (Trial A), trees on the rootstocks in the former group bore only twice the number of trusses per centimetre of new wood borne by the trees in the latter group.

It does appear, nevertheless, that the trees in the more vigorous Group 5 are relatively much less productive assessed on this basis, even at six years old, than are those on the rootstocks in the more dwarfing Groups 2 and 3, and that the much greater aggregate blossom formation of the trees on the more vigorous rootstocks, by the end of their sixth year, is to be attributed chiefly to the relatively greater areas of potential blossom bearing surface available and, only to a minor degree, to a slight increase in the inherent productiveness, with advancing age, of these trees.

(c) Early Evidences of Precocity.

In the preceding section it has been shown that the correlation between early inherent productiveness and the dwarfing effect, which is, in general, markedly shown in the Malling series of " Paradise " rootstocks, can be extended beyond Hatton's dwarfing group, represented in these trials by Malling No. IX, to the extra dwarfing rootstocks obtained in some of the seedlings in the family raised from VIII × IX. As may be seen from Table V, the trees on the rootstocks in Groups 1, 2 and 3, in Trial C, bore, over their first three years, on the average, an approximately equal number of trusses, and the superior productiveness of the trees on the rootstocks in Group 1 compared with those in Group 2, or of those in Group 2 when compared with the trees in Group 3, cannot be shown, even at this relatively early stage, until the differential effect

of tree size has been eliminated. It is, however, possible to demonstrate the greater actual productiveness of the trees on the rootstocks in these dwarfing groups, in spite of their smaller size, at an earlier stage. In Table VII the average

TABLE VII.

Average Number of Blossom Trusses in First Year.

Rootstock No.	Trial A. Budded in 1930.	Trial B. Budded in 1932.	Trial C. Budded in 1933.
Group 1.			
70	—	—	15·2
15	—	—	16·9
99	—	16·6	16·4
Average :	—	**16·6**	**16·2**
Group 2.			
109	2·2	—	15·7
93	1·0	—	13·1
22	2·7	—	15·3
29	1·8	13·9	16·5
96	—	—	17·2
Average :	**1·9**	**13·9**	**15·6**
Group 3.			
IX	4·0	13·1	12·5
108	0·8	15·6	11·3
9	0·6	11·9	7·9
Average :	**1·8**	**13·5**	**10·6**
Group 4.			
116	—	—	6·2
90	—	9·2	9·8
VII	—	8·9	3·7
Average :	—	**9·1**	**6·6**
Group 5.			
128	—	6·3	2·8
122	—	—	1·6
125	1·5	7·2	3·0
112	1·1	7·8	2·9
45	0·1	5·2	1·6
119	—	—	2·2
89	0·9	—	4·1
Average :	**0·9**	**6·6**	**2·6**

number of trusses per tree, borne in the spring following the end of their maiden year by the trees on all these rootstocks are shown. The result is perhaps more striking in diagrammatic form and, in Diagram B, the trees in Trial C are shown in this way. There is very clear evidence that the trees on the rootstocks. in these five groups, in their first blossoming season, showed a marked decrease in productivity associated with increase in vigour even in the most dwarfing

groups. Thus, the trees on the rootstocks in Group 1, Trial C, produced at this age, on the average, 0·6 more trusses than did the trees in Group 2, while the latter produced five more trusses per tree than did those in Group 3.

Although it would be decidedly premature at this stage to attempt to draw any very definite conclusions as to the relative productivity of the rootstocks in this series compared with those in the Malling "Paradise" series, certain general tendencies have become sufficiently marked to deserve comment. Thus, although trees on all the eight rootstocks in this series, more dwarfing than

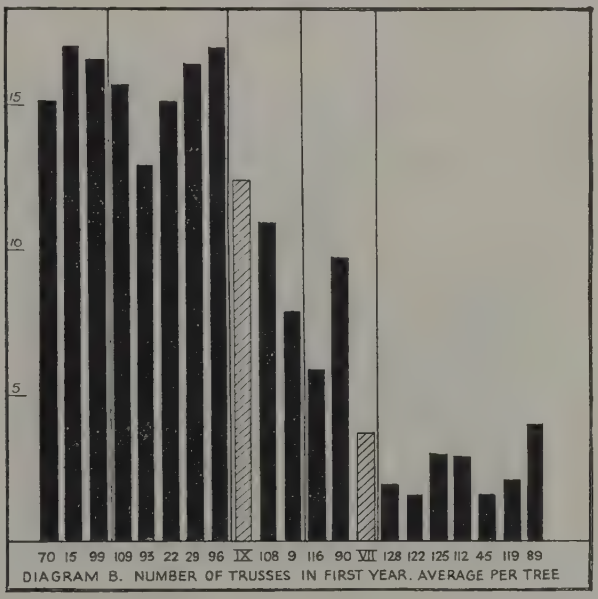

DIAGRAM B. NUMBER OF TRUSSES IN FIRST YEAR. AVERAGE PER TREE

Malling No. IX, in the same trial, had borne a greater aggregate of trusses in their first season, by the end of their third year the trees on No. IX were more prolific than all except one of them. By the end of their sixth year, in Trial A, trees on the other two rootstocks in Group 3, and those on the four rootstocks in Group 5, had all borne a larger number of trusses than had the trees on No. IX, while those on the four rootstocks in Group 2 had borne fewer. This result is intimately bound up with relative tree size. Assessed on the basis of trusses produced per unit of new wood, eight of these rootstocks have been found to be more productive, up to their third year, than Malling No. IX.

The trees on Malling No. VII, growing in Trial C, bore fewer trusses than those of all, except one, of the rootstocks in the series. In Trial B, on the other hand, at the end of their fourth year, they were among the most prolific, having

borne considerably more trusses than those on Malling No. IX. As Table VI shows, however, on the basis of the trusses borne per unit of new wood, Malling No. VII was about equally productive with the other rootstocks in the same vigour-group at the end of its third and fourth years.

(d) As Measured by Fruit Production.

The fruits were counted and weighed each year. The total weights up to the end of the third, fourth and sixth years respectively are summarized in

Table VIII.

Average Total Crop per Tree in Pounds.

Rootstock No.	Trial A. Budded in 1930. Six years total.	Trial B. Budded in 1932. Four years total.	Trial C. Budded in 1933. Three years total.
Group 1.			
70	—	—	5·0
15	—	—	4·9
99	—	2·6	5·0
Average :	—	**2·6**	**5·0**
Group 2.			
109	15·2	—	4·1
93	30·1	—	5·1
22	23·2	—	4·5
29	13·2	2·8	5·4
96	—	—	4·5
Average :	**20·5**	**2·8**	**4·7**
Group 3.			
IX	20·6	2·7	5·6
108	21·6	2·8	4·4
9	20·3	2·5	4·4
Average :	**20·9**	**2·6**	**4·8**
Group 4.			
116	—	—	3·6
90	—	2·7	4·7
VII	—	1·2	2·4
Average :	—	**2·1**	**3·6**
Group 5.			
128	—	1·4	2·1
122	—	—	2·5
125	23·4	1·4	2·7
112	21·0	1·4	2·3
45	23·2	1·0	3·0
119	—	—	2·9
89	30·3	—	3·0
Average :	**24·4**	**1·4**	**2·6**

Table VIII and those for the rootstocks in Trial C are shown in Diagram C. The rootstocks are arranged in both cases in order of increasing vigour in the five vigour-groups. At the end of three years, the trees on Malling No. IX (in Trial C), had actually borne a greater weight of fruit, on the average, than had those on any of the rootstocks in the VIII × IX series. In general, however, and in spite of minor exceptions, there is a very close correlation between tree size and crop. Thus, the trees on the three rootstocks in Group 1 bore,

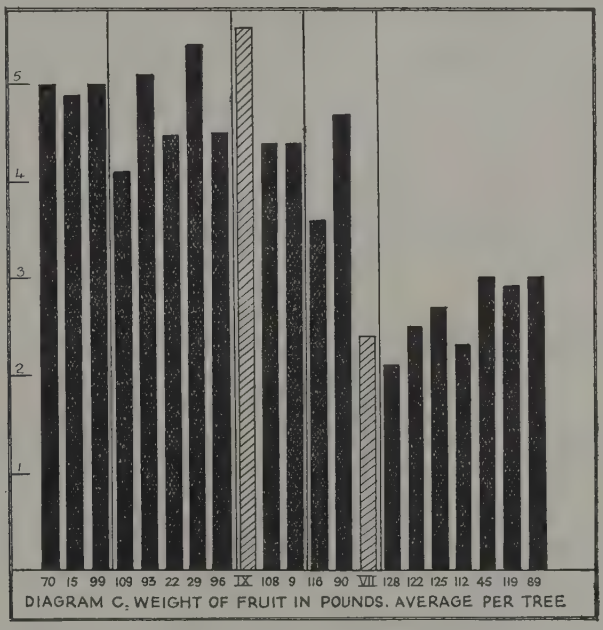

DIAGRAM C. WEIGHT OF FRUIT IN POUNDS. AVERAGE PER TREE.

over the three years, a total of 5 lb. of fruit per tree, while, at the other extreme, the trees on the seven rootstocks in Group 5, bore approximately half this amount. Between these two extremes the trees on the rootstocks in the various groups can be arranged in a strikingly regular series. Among the four year old trees, in Trial B, this tendency can still be seen, although the differences between the trees on the rootstocks in the first three groups had to some extent disappeared.

Up to the end of their sixth year, the trees on the rootstocks in the vigorous group, in Trial A, had borne a somewhat greater weight of fruit than had the trees on the rootstocks in the less vigorous groups. This result is, of course, in line with that obtained with respect to blossom formation and arises from the same causes.

Seven of the ten rootstocks of the VIII × IX series, planted in Trial A, yielded a greater weight of fruit than did the trees on Malling No. IX, growing in the same trial, in their first six years. Actually the trees on No. 93, slightly more vigorous in this particular trial and at this age than were the trees on the dwarfing Malling No. IX, produced, in the six years, almost 10 lb. more fruit per tree than did the trees on Malling No. IX. In the vigorous group, the trees on No. 89 also produced, during this period, an average of almost 10 lb. more fruit than the trees on Malling No. IX. Since the conditions under which the trees in this trial were growing were not as uniform as in the later trials, these results must not be regarded as more than an indication of the economic possibilities of this series.

It is interesting to notice the close association between the "dwarfing" character and "precocity", so very marked in the rootstocks in this series. The fact that two such "precocious" rootstocks as Malling Nos. VIII and IX when crossed gave rise to seedlings not only apparently much more "precocious" but also much less "precocious" than themselves, is yet another indication of their very heterozygous constitution.

III. THE INFLUENCE OF THE ROOTSTOCK ON THE HEALTH OF THE SCION.

Since the casual incidence of outbreaks of diseases and pests might introduce a differential element into the trials, careful records were kept of their occurrence.

TABLE IX.

Relative Susceptibility to Leaf Scorch. Average per Tree.

Rootstock No.	Relative severity of attack.*
45	0·275
9	0·425
128	0·425
90	0·425
112	0·475
125	0·475
29	0·625
IX	0·625
99	0·675
108	0·800
VII	1·700

* The trees were marked in order of increasing severity of scorching from 0=no scorching to 10=very severe scorching indeed. The above figures are the averages of 50 trees in each case. The brackets in Tables IX, XI and XII indicate that there was no statistically significant difference between the rootstocks within them.

Such data might provide evidence of a definite influence of the rootstock upon the resistance or susceptibility to disease of the scion and of the practicability or otherwise of breeding rootstocks capable of imparting resistance to or immunity from disease to the scion. The results set out in the Tables which follow were, in most cases, based on observations made during a single season and, while they illustrate the range of variation in relative susceptibility, they may be subject to modification in subsequent years.

TABLE X.

Number of Clean and Scabbed Fruits expressed as a Percentage of the Total Number of Fruits. Average per Tree.

Rootstock No.	Trial B.				Trial C.			
	Clean.	Slight.	Moderate.	Severe.	Clean.	Slight.	Moderate.	Severe.
Group 1.								
70	—	—	—	—	64·1	24·3	7·1	4·5
15	—	—	—	—	76·2	17·2	4·8	1·8
99	80·6	13·4	4·8	1·2	61·5	22·9	13·3	2·3
Average :	**80·6**	**13·4**	**4·8**	**1·2**	**67·3**	**21·5**	**8·4**	**2·8**
Group 2.								
109	—	—	—	—	71·8	18·9	8·4	0·9
93	—	—	—	—	73·4	19·2	6·8	0·6
22	—	—	—	—	73·4	15·9	8·4	2·3
29	91·5	6·8	1·4	0·3	67·7	22·8	8·0	1·5
96	—	—	—	—	64·6	24·6	9·2	1·6
Average :	**91·5**	**6·8**	**1·4**	**0·3**	**70·2**	**20·3**	**8·1**	**1·4**
Group 3.								
IX	89·2	8·2	2·3	0·4	68·5	20·0	9·6	1·9
108	85·0	10·9	2·2	1·9	72·9	20·9	4·9	1·3
9	83·8	12·3	3·2	0·7	69·9	20·0	8·3	1·8
Average :	**86·0**	**10·5**	**2·5**	**1·0**	**70·4**	**20·3**	**7·6**	**1·7**
Group 4.								
116	—	—	—	—	72·4	21·2	5·0	1·4
90	91·0	5·0	3·8	0·3	79·0	13·5	6·2	1·3
VII	82·7	11·4	5·3	0·6	78·0	15·1	6·2	0·7
Average :	**86·8**	**8·2**	**4·5**	**0·5**	**76·5**	**16·6**	**5·8**	**1·1**
Group 5.								
128	91·4	4·7	1·8	2·1	85·0	9·8	5·2	0
122	—	—	—	—	83·9	11·1	4·5	0·5
125	96·4	2·8	0·4	0·4	79·2	13·8	6·3	0·7
112	94·2	5·8	0	0	74·4	17·9	6·8	0·9
45	96·2	1·7	1·1	1·0	82·3	13·5	3·3	0·9
119	—	—	—	—	74·6	17·9	6·6	0·9
89	—	—	—	—	71·4	20·2	6·8	1·6
Average :	**94·6**	**3·7**	**0·8**	**0·9**	**78·7**	**14·9**	**5·6**	**0·8**

(a) Leaf Scorch.

During the summer of 1936, the trees in Trial B showed considerable scorching of the leaves, and a record was made of its relative intensity. The records are summarized in Table IX. The trees were given marks from 0 to 10 according to the severity of the trouble. Those on No. 108, the most severely affected, were about three times as badly scorched as were the trees on No. 45, the least severely affected. The trees on Malling No. VII were more than twice as severely scorched as were the trees on No. 108. A statistical examination of the records suggests that the trees on some of these rootstocks may be markedly more resistant to this trouble than those on others. This has already been proved in the Malling series of "Paradise" stocks.

(b) Apple Scab.

The fruits obtained from the trees in the three trials were graded according to the severity of attack by Scab during 1936. The results for Trials B and C are summarized in Table X. The rootstocks have been arranged in order of increasing vigour in the five groups and, as the Table shows, there was a very distinct correlation, in the two trials, between the vigour of the trees and the relative amount of Scab on the fruits. Thus, in Trial C, while the three rootstocks in Group 1 bore only 67·3% of clean fruit, the percentage of clean fruit on the trees on the seven rootstocks in the vigorous Group 5 was about 79. Between these extremes there was a gradual but fairly regular increase in the proportion of clean fruit with increasing vigour of the rootstock. This result is equally pronounced in the trees in Trial B, but was less obvious in the older trees in Trial A, probably because these trees, not being grown in randomized blocks, were more susceptible to positional influences. The causes of this very striking relation between increase of vigour and decrease of Scab-infection are rather obscure, but there is little evidence that any of these rootstocks are likely to be capable of imparting to the scion outstanding resistance to Scab.

(c) Apple Canker.

There was a fairly severe attack of Canker on the trees in Trial C during 1936, and records were made of its severity. In Table XI are shown the number of cankered shoots as a percentage of the total number of shoots on the tree. The average of forty trees is given for each rootstock. The trees on these rootstocks showed a wide range of variation in their susceptibility to this disease. Thus, the trees on No. 15 were, on the average, almost twenty times as severely cankered as were the trees on No. 112. These results suggest the possibility that the rootstock was exerting a differential effect on the scion, but they may possibly be attributable to other causes.

Table XI.

Number of Cankered Shoots expressed as a Percentage of the Total Number of Shoots. Average per Tree.

Rootstock No.	Percentage number of Cankered Shoots.
112	0·234
119	0·878
109	1·113
89	1·153
9	1·178
108	1·228
125	1·316
122	1·431
22	1·444
116	1·513
VII	2·147
45	2·319
99	2·350
IX	2·544
29	2·581
15	4·044

(d) Apple Mildew.

Attacks of Mildew were of frequent occurrence in these trials. It was relatively more serious, however, on the trees in Trial B, which had never made so much growth as had the trees in A and C. The severity of attack was recorded during 1936 and the results are summarized in Table XII. The number of shoots on each tree actually mildewed were calculated as a percentage

Table XII.

Number of Mildewed Shoots expressed as a Percentage of the Total Number of Shoots. Average per Tree.

Rootstock No.	Percentage number of mildewed shoots.
90	2·46
125	3·67
99	4·19
112	4·49
108	4·82
45	4·90
IX	5·49
9	5·52
128	7·35
29	7·74
VII	9·64

of the total number of shoots on the tree. Although the trees on No. 29 were actually about three times as severely affected as were those on No. 90, there was no statistically significant difference between the trees on the nine VIII x IX rootstocks shown in the Table. Such differences as were found were presumably due to chance.

(e) Crown Gall.

During extensive tree excavations in the winter of 1936, the incidence of Crown Gall on the roots of the trees in Trial B were recorded. The trees on No. 108 had large galls in almost every instance, but they were not found to any marked extent on any of the other rootstocks. It may be added that "burr knots" were of frequent occurrence on the stock-stem portion of the trees on No. 112. So far as is known, there is no connection whatever between Crown Gall and "burr knots".

(f) Apple Blossom Weevil.

An exceptionally severe infestation of Blossom Weevil occurred in Trial C during the spring of 1936. The "capped" blossoms were counted and the results are summarized in Table XIII. The figures in the Table are based on an average of forty trees on each rootstock and the number of "capped" blossoms is expressed as a percentage of the total number of blossoms on the tree. The rootstocks have been arranged in order of increasing vigour in the five groups.

The trees on the more vigorous rootstocks were relatively more severely attacked than those on the more dwarfing rootstocks. There was a fairly regular gradation in severity of infestation between the trees on the most dwarfing rootstocks in Group 1 and those on the most vigorous rootstocks in Group 5. This result appeared to be quite definitely related to the time at which the trees on the different rootstocks opened their blossoms. It had always been observed in these trials that the trees on the more dwarfing rootstocks were in full blossom some considerable time before the trees on the more vigorous rootstocks. It is thought that the most severe infestation of Weevils occurred, in this particular year, after the blossoms on the trees on the more dwarfing rootstocks were open, and while those on the trees on the more vigorous rootstocks were still in bud.

It may be said that so far as the limited observations on these trees have gone, little definite evidence of a direct influence of the rootstock on the resistance to disease of the scion has been obtained. In two instances, those of Scab and Blossom Weevil, a direct correlation between the size of the tree and

TABLE XIII.

Number of "Capped" Blossoms expressed as a Percentage of the Total Number of Blossoms. Average per Tree.

Rootstock No.	Percentage number of "Capped" Blossoms.
Group 1.	
70	9·2
15	8·1
Average :	**8·6**
Group 2.	
109	3·0
93	8·2
22	9·6
29	5·5
96	9·1
Average :	**7·1**
Group 3.	
IX	12·9
108	12·7
9	15·9
Average :	**13·8**
Group 4.	
116	14·8
90	10·6
VII	22·0
Average :	**15·8**
Group 5.	
128	20·3
122	10·0
112	22·3
119	20·7
89	19·4
Average :	**18·5**

relative freedom from infestation has been established. In the former, increase in size of tree was associated with a progressive freedom from disease, while in the latter the larger trees were those most severely affected. Quite obviously the underlying cause in the two cases was quite different. With Leaf Scorch, Canker and Mildew, such results as have been obtained do not suggest that any of the rootstocks in this series were capable of imparting any very definite resistance to the particular scion used, although the rootstocks do appear to exert slight differential effects on the relative resistance of the scion to Leaf Scorch and Canker. Only with Crown Gall on the roots was it possible to find a clear instance of the susceptibility of one particular variety of rootstock.

THE MORPHOLOGY OF THE ROOT SYSTEMS.

Some interesting morphological differences, principally in the relative amount and position of the fibre on the root systems of trees growing on certain of these rootstocks, were noted when the trees in Trial B were excavated during the winter of 1936-7. They are fully reported on elsewhere (9).

The writer's sincere thanks are due to Miss J. L. Edgar for much assistance from the statistical side and to all those members, past and present, of the recording staff at East Malling, without whose unstinted help his task would have been impossible. Finally, he is indebted to Miss K. Cornford for the photographs.

SUMMARY.

This paper describes studies, extending over six years, of trees worked on nineteen selected rootstocks from a family, Malling No. VIII (French Paradise) x Malling No. IX (Jaune de Metz), raised at the John Innes Horticultural Institution in 1923.

It is shown that there was an extremely wide range of variation in vigour between the trees of Lane's Prince Albert worked upon these rootstocks, whether expressed in terms of the new wood made, increase in thickness of the stems or the ultimate weight of the tree.

It was found possible to classify the rootstocks into five "vigour" groups. The rootstocks in two of these were found to exert an even more dwarfing effect on the tree than did the dwarfing Malling No. IX, growing in the same trials. At the other extreme, seven of the rootstocks exerted a definitely more vigorous effect than Malling No. VII at three years old.

A very close relation is shown to exist between the vigour of the trees on these rootstocks and the relative size of the swelling at the union.

When expressed in terms of blossom production, very considerable differences were found in the relative productivity of the trees on the various rootstocks. A very clear and consistent correlation was found to exist between the "dwarfing" character and the productivity of the trees, the trees on the more vigorous rootstocks being, in every case, less productive, in their earlier years, than those on the more dwarfing rootstocks.

Although, in regard to the actual number of blossom trusses produced by the end of the third year, there was little perceptible difference between the trees on the rootstocks in the three least vigorous groups, it was possible to

demonstrate the greater relative precocity of the trees on the most dwarfing rootstocks, on the basis of the blossom trusses produced per unit of new wood growth.

In the first year of flowering, the trees on the most dwarfing of the series bore a considerably larger number of blossom trusses than did the trees on Malling No. IX growing in the same trials.

Records of fruit production by the trees on these rootstocks are summarized and discussed. It is shown that, in general, the conclusions that can be drawn approximate very closely to those already outlined for blossom truss production.

Data are given showing the relative susceptibility of the trees, during a single season, to Leaf Scorch, Scab, Canker, Mildew, Crown Gall and Blossom Weevil. Little evidence of a direct rootstock influence on the degree of attack on the scion could be deduced. A somewhat obscure correlation between the vigour of the tree and the relative freedom of its fruit from Scab is mentioned and an instance is given of the effect on the severity of apple Blossom Weevil attack on different rootstocks, due, probably, to the varying times at which the flowers on the trees growing on them opened.

REFERENCES.

(1) *Hatton, R. G.* Paradise Apple Rootstocks. Journ. Roy. Hort. Soc., 1917, **42**, 361-99.

(2) ———. The Influence of Different Rootstocks upon the Vigour and Productivity of the Variety Budded or Grafted Thereon. Journ. Pom. & Hort. Sci., 1927, **6**, 1-28.

(3) ———. The Relationship Between Scion and Rootstock with Special Reference to the Tree Fruits. Masters' Memorial Lecture for 1929. Journ. Roy. Hort. Sci., 1930, **55**, 169-211.

(4) ———. Apple Rootstock Studies: Effect of Layered Stocks upon the Vigour and Cropping of Certain Scions. Journ. Pom. & Hort. Sci., 1935, **13**, 293-350.

(5) *Le Pelley, R. H.* Studies on the Resistance of Apple to the Woolly Aphis. Journ. Pom. & Hort. Sci., 1927, **6**, 209-41.

(6) *Tydeman, H. M.* Apple Rootstocks Immune from Woolly Aphis. A Progress Report on Trials with New Varieties. East Malling Res. Sta. Ann. Rpt. for 1934 (1935), 115-22.

(7) *Crane, M. B., Greenslade, R. M., Massee, A. M.* and *Tydeman, H. M.* Studies on the Resistance and Immunity of Apples to the Woolly Aphis. Journ. Pom. & Hort. Sci., 1936, **14**, 137-63.

(8) *Crane, M. B., Greenslade, R. M., Hatton, R. G., Massee, A. M., Roach, W. A., Rogers, W. S.* and *Tydeman, H. M.* Problems raised by the Woolly Aphis of the Apple. Papers read before the Association of Applied Biologists, October, 1936. Annals of Applied Biology, 1937, **24**, 169-210.

(9) *Tydeman, H. M.* The Root Systems of Some New Varieties of Apple Rootstock. East Malling Res. Sta. Ann. Rpt. for 1936 (1937), 87-91.

(*Received* 20/3/37.)

FIG. 1.

Lane's Prince Albert on Rootstock No. 125 (Vigorous Group).
Six year old tree.

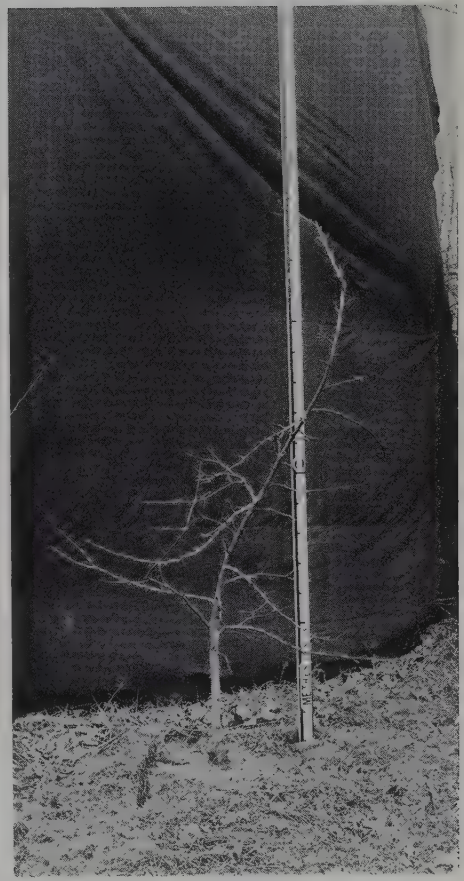

FIG. 2.

Lane's Prince Albert on Rootstock No. 109
(Dwarfing Group).
Six year old tree.

A CASE OF UNFRUITFULNESS IN BLACK CURRANTS

By MARIE LEDEBOER and I. RIETSEMA

(R.K. Land- en Tuinbouwschool, Breda)

I. Introduction.

The attention of the writers having been drawn to a black currant plantation in Belgium, in which almost the whole crop of fruit was said to "run off" each year, observations were made during 1934, 1935 and 1936 which showed that this was true of one particular variety, the flowers and young fruits of which dropped to such an extent that the crop was a failure. This variety formed the greater part of the plantation, although there were also present in it a considerable number of bushes of Goliath, a few of Boskoop Giant and of some other undetermined varieties. The "running off" did not occur in Goliath (apart from the dropping of frozen flowers) but there were not enough bushes of Boskoop Giant to form an estimate. Of the remaining varieties some showed severe "running off", others set fruit excellently.

The variety in question was readily recognized as that known in Holland as Lee's Prolific, which was described and illustrated in the 1926-7 Report of the Experiment Garden at Breda (4). In Holland it was already known that this name was not the correct one for this variety, which, indeed, proved to be identical with one named Lee's Schwarze, introduced into Holland from a well-known nursery in Germany about 1920. The variety was compared with English material of Lee's Prolific, kindly supplied by Dr. Hatton, of East Malling, but was found to differ distinctly from that. Up to the present it has not been possible definitely to identify the variety; in the present paper it will be referred to simply as Lee's.

The "running off", or "coulure" as it is called in Belgium, was characterized by dropping of the fruit at an early stage, viz. a week or so after flowering. At that period the ground beneath the Lee's bushes was covered with fallen, unripe fruits and withered flowers. On some of the racemes no fruit at all was left, and dropping occurred equally from the terminal and basal parts of the racemes.

II. Causes of Unfruitfulness.

Premature shedding of fruits may be due to several causes. Crane and Lawrence (6, 7) have discussed generational and morphological sterility as well as incompatibility in this connection. Sometimes sterility may be due to fungus attack, as shown by Bennett (3) for wheat and by Dearness and Foster (9) for

loganberry. Insect attacks may also lead to barrenness. The virus disease of black currants known as Reversion is inimical to the setting of the fruit, and Ridler (16) showed that abnormal ovaries and ovules are associated with it. Hatton and Amos (12) pointed out that one of the symptoms of Reversion is the production of abnormal flowers. "Running off" of black currants was shown by Wellington, Hatton and Amos (19) to be due to the disproportionate length of the styles, and consequent pollination failure. Finally, spring frosts and also high temperatures prevailing during the flowering period are injurious to the flowers and young fruits.

The investigations now to be described were undertaken to ascertain the cause underlying the failure of the Lee's black currant in the Belgian plantation to crop.

III. Investigation Work.

(1) *Material used.*

Authentic cuttings of what will be designated as Lee's B, taken from the Belgian plantation in summer, were struck. They were grown in small pots during the winter preceding the spring in which the experiments were started. Similar material of Goliath was available and, in addition, cuttings of Lee's secured from two other plantations (here designated as Lee's Li and Lee's O) were used for purposes of comparison. Towards the end of February, 1935, the material was placed in a moderately warm glasshouse in the experimental garden at Breda, and the cuttings were gently forced into bloom towards the end of March. The pots stood plunged in a layer of peat dust, kept continuously moist, on the cement floor of the glasshouse. In the first season each cutting produced an average of three racemes of flowers. As soon as possible after ripening their fruit the cuttings were transferred to larger pots and placed out of doors, where they remained until the following spring. During the summer they made considerable growth, and they were kept in condition by watering with Wagner's solution (18). It was noted that the flower buds for the following season were borne on those parts of the shoots that had developed in the open air. In 1936 these plants each produced an average of about 100 flowers. They set their fruit much better than in the previous year, and better than other Lee's cuttings fruiting for the first time in 1936. Their set of fruit in the greenhouse was similar to that of full grown Lee's bushes (known to have been derived from the Belgian plantation) in the open air in a Dutch plantation near the Belgian border.

(2) *Crosses carried out.*

In trials carried on over four consecutive years, Wellington, Hatton and Amos (19) found that the four chief groups of black currants (Boskoop Giant,

French, Baldwin and Goliath) were self-compatible. They found, however, one variety only (Baldwin) that was unaffected by the exclusion of insect visitors. Lack of such visitors may lead to complete failure to fruit in certain varieties. As to Lee's, its tendency to "run off" and its failure to crop when insects are excluded have already been noted in Holland (4).

TABLE I.

Variety.	Pollinated with	No. of flowers pollinated.	No. of fruits set.	% of fruits set.
Lee's B	Various Lee's	329	2	1
,,	Lee's B	23	0	0
,,	Lee's Li	56	0	0
,,	Lee's O	40	0	0
,,	Goliath	262	54	21
,,	Boskoop	40	3	7
,,	Roodknop	17	2	12
Lee's O	Various Lee's	115	0	0
,,	Lee's B	32	0	0
,,	Lee's Li	79	2	3
,,	Lee's O	30	1	3
,,	Goliath	62	12	19
,,	Boskoop	74	11	15
Lee's Li	Various Lee's	163	8	5
,,	Lee's B	20	0	0
,,	Lee's Li	36	0	0
,,	Lee's O	27	0	0
,,	Goliath	159	40	25
,,	Boskoop	45	14	31
,,	Roodknop	25	5	20
Goliath	Various Lee's	27	16	59
,,	Lee's B	69	33	48
,,	Lee's Li	33	9	27
,,	Lee's O	77	27	35
,,	Goliath	55	33	60
,,	Boskoop	39	13	33
,,	Roodknop	18	8	44
Boskoop	Lee's B	30	14	47
,,	Lee's Li	40	19	47
,,	Lee's O	53	20	38
,,	Goliath	6	3	50
,,	Boskoop	27	4	15
,,	Roodknop	11	0	0
Roodknop	Lee's B	24	14	58
,,	Lee's Li	14	3	21
,,	Lee's O	37	14	38
,,	Goliath	4	2	50
,,	Boskoop	26	17	65

To investigate this variety more fully, as large a number as possible of self- and cross-pollinations were made with it. Pollination was effected by removing a stamen with a pair of forceps from a recently opened flower and rubbing its anther against the viscid stigma of the flower to be pollinated. The pollen adhered well.

A start was made with the potted cuttings in the glasshouse in the spring of 1935, these being artificially pollinated. At the same time their own pollen was applied to the stigmas of flowers of other varieties. Often all the flowers of the different racemes on one plant were pollinated with pollen from a different variety, to serve as checks. The results of the crosses were judged by the number of ripe fruits produced and are expressed as percentages of the number of flowers to which pollen of a definite variety had been applied. They are assembled in Table I.

Summing up the relevant figures from this Table it will be found that Lee's, when selfed, set only 1% of fruit, whereas when crossed with Goliath it set 22%. Goliath, when selfed or crossed, set 48%. These figures are somewhat low when compared with those of larger plants, as will be seen later, but the difference between the selfed and crossed Lee's is very marked. It is also clear from the Table that the self-sterility of Lee's cannot be due to incompetence of its pollen, for that pollen was satisfactory when used with other varieties. It might be suspected from the figures that Lee's pollen on Goliath was slightly inferior to Goliath pollen on Goliath, but the results obtained in the following year, 1936, did not support this view.

The crosses made in 1935 were repeated in 1936 in the glasshouse on some of the same Lee's cuttings as well as on certain others, and the results are given in Table II.

TABLE II.

Variety.	Pollinated with	No. of flowers pollinated.		No. of fruits set.		% of fruits set.	
Lee's B New cuttings ..	Lee's B ..	113		0		0	
,, ,, ..	*Lee's E.M. ..	82	652	8	87	10	12
,, ,, ..	Goliath ..	459		58		13	
,, ,, ..	Boskoop ..	107		18		17	
,, ,, ..	Baldwin ..	4		3		75	
Lee's B Old cuttings ..	Goliath ..	261		104		40	
Lee's Li ,, ..	Lee's Li ..	435		0		0	
,, ,, ..	Goliath ..	489		210		43	
Lee's O ,, ..	Lee's O ..	394		2		0·5	
,, ,, ..	Goliath ..	519		162		31	

* Lee's Prolific, from East Malling, a different variety from the Belgian Lee's.

Here, again, it is seen that in the new cuttings Lee's, when selfed, produced no fruit. When crossed with Goliath the set was only 13% and the average with all foreign pollinations was 12%. The cuttings were probably not as well rooted as in 1935. On one young Goliath cutting, however, 7 flowers pollinated with Lee's pollen produced 6 ripe fruits. In the old cuttings the results are

still more striking and also more trustworthy, on account of the greater vigour of the plants and the larger number of flowers pollinated. They show clearly the necessity of foreign pollen for fruit production in Lee's (see Fig. 1). The quality of Lee's pollen was again tested by using it on Goliath, when 85% of ripe fruits were obtained, showing its competence.

Another series of pollinations was carried out in 1935 on bushes in the open in a mixed plantation of Lee's and Goliath. The branches used in the trials were encased in muslin ("Victoria lawn") sleeves, stretched on wire frames, just before the flowers began to open. As soon as opening started the flowers were emasculated. At least every second day the encased branches were examined, and thus the opening flowers were dealt with successively. Any flowers found in which the anthers had already dehisced were at once removed and eliminated from the experiment, thus avoiding unintentional self-pollination and the risk of possible antagonistic influence on the applied pollen, as found in cotton by Kearney and Harrison (14). The flowers were pollinated either on the same day as emasculation or on the following one by placing a small quantity of the required pollen on their stigmas.

In 1935, flowers of Lee's only were thus artificially pollinated. Three branches on different bushes were used for the Lee's pollen trial, and three others on the same bushes as well as one branch on each of three other bushes for Goliath pollen. Pollination was effected between May 1st and 8th, the coverings were removed on May 14th and the number of fruits was determined on June 28th, when they were already black. The results are given in Table III.

TABLE III.

Variety.	Pollinated with	No. of flowers pollinated.	No. of fruits set.	% of fruits set.
Lee's ..	Lee's ..	255	8	3
,, ..	Goliath ..	611	276	45

From this it is seen that the setting of fruit when Lee's is selfed is almost negligible as compared with that following crossing with Goliath.

These trials were repeated on the same bushes in 1936. Muslin was used for covering some of the branches, cellophane for others, whilst some branches were not encased at all. The results are given in Table IV and illustrated in Fig. 3.

Thus, selfing again produced very little set of fruit, whilst crossing with Goliath, whether under muslin or cellophane, resulted in a good set, better than in the previous year, possibly because the weather was cooler in May, 1936, than in 1935, when the first week of May was very hot and sunny. In the

Table IV.

Variety.	Pollinated with	No. of flowers pollinated.	No. of fruits set.	% of fruits set.
Lee's ..	Lee's (in muslin) ..	665	19	3
,, ..	Goliath (in muslin) ..	177	110	62
,, ..	Goliath (in cellophane) ..	146	89	61
,, ..	Goliath (in the open) ..	132	45	34
,, ..	(bee pollinated in the open)	1,330	624	46

relatively cold May of 1936 the muslin and cellophane coverings may have been an advantage ; this may explain why the set of flowers in the open crossed with Goliath was little more than half of that of the covered ones. On the whole, artificial pollination gave a better set of fruit than natural pollination by insects.

In 1937 the results of all pollinations confirmed those of 1935 and 1936. Lee's B, with its own pollen, set 0·1% of fruit from 951 flowers in the glass-house (checks 30% from 960 flowers) and 1% of fruit from 1,074 flowers under cover in the open (checks 40% from 694 flowers). In the plantation itself, artificial pollination with Goliath pollen gave a set of 53% of fruit from 377 unprotected flowers against 11% from 290 flowers following bee pollination on the same bushes.

In order to ascertain whether the Lee's and the Goliath pollen was vigorous, collections were made in Belgium and applied on the next day to emasculated flowers in Breda. The results were :—

Variety.	Pollinated with	No. of flowers pollinated.	No. of fruits set.	% of fruits set.
Goliath ..	Lee's ..	50	47	94
Lee's ..	Goliath ..	57	34	60

Thus, the pollen of Lee's from the Belgian plantation was perfectly efficient, and the Goliath pollen gave the same results as those obtained with it in previous trials. The reduced set obtained from Goliath pollen on Lee's must be looked on as due to some special character in Lee's ; it is certainly not due to faulty experimental methods.

The differences between selfed and crossed flowers are still more marked when the average weights of the fruits are compared. Thus, the average berry weight of Lee's selfed was 0·22 gm. in 1935, and 0·28 gm. in 1936 ; that of Lee's crossed with Goliath was 0·61 in 1935 and 0·99 in 1936. The berries of insect-pollinated Lee's averaged 0·36 gm. Flowers left to natural pollination

apparently suffered from a shortage of Goliath pollen and consequently did not produce large fruits.

Another experiment made in 1936 was with a single potted bush of Lee's. Some of the branches were exposed to insect visitors during the flowering period in immediate proximity to open Goliath flowers, others stood fairly near such flowers and still others a long distance from them. The pot was moved several times to obtain the necessary locations, and the branches exposed in one situation were encased when exposed in the two others. The results were as follows:—

TABLE V.

Situation of Plant.	Branches.	No. of flowers.	No. of fruits set.	% of fruits set.	
Close to Goliath ..	a	42	31	74	
Close to Goliath ..	b	11	7	64	42
Fairly near Goliath ..	c	26	0	0	
Fairly near Goliath ..	d	23	5	22	
Far from Goliath ..	e	72	4	6	
Far from Goliath ..	f	48	5	14	9
Far from Goliath ..	g	41	6	15	

The weather conditions during the experiment were not favourable to the visits of bees, but from the figures given it can be seen that when very near or comparatively so to Goliath, the set of fruits was about 42%, whilst at a great distance from this variety the set was only 9%, thus showing the importance of cross pollination in Lee's.

(3) *Similar behaviour in other Ribes Varieties.*

Amos (1) has reported "the almost total failure of the rogue types to set fruit", but the cause of this does not yet appear to be clear. Further, according to Tydeman (17), "running off" is rather common in the seedlings of certain varieties. One variety of Ribes ("Groseillier sans pépin") was already known to the present writers to exhibit very incomplete setting of the fruit in the experimental garden at Breda, and it was thought that the cause might be the same as that in Lee's. A single pollination experiment with this variety settled the question. From 750 selfed flowers only 131 fruits (17%) were obtained; from 854 flowers crossed with the pollen of different varieties of red currant, 322 fruits (39%) resulted. This difference is sufficient to warrant the conclusion that foreign pollen is a remedy for the poor fruiting of "Groseillier sans pépin". The similarity in behaviour to Lee's is more striking when the weights of the berries are considered. Selfed flowers yielded fruits averaging 0·44 gm. in weight, each containing a single seed; crossed flowers gave berries averaging 0·81 gm., containing five seeds each.

(4) *Mycological aspects.*

It was thought possible that fungi might be responsible for the failure of Lee's to set fruit, one species (which was isolated and identified as *Cladosporium herbarum*) having been observed on the styles and between the pollen in the flowers of both Lee's and Goliath in the Belgian plantation in 1934. This fungus is usually regarded as a mere saprophyte, but spores of it were placed on the stigmas of flowers of both varieties a day or two before, just prior to, just after and a day after the application of Lee's pollen to both varieties, and Goliath to Lee's. With the former the number of fruits set in the presence of the spores was in both varieties slightly greater than in the controls to which no spores had been added. With Goliath pollen, the number was slightly less, but the difference was not significant enough to suggest any injurious effect from the presence of the fungus. In one instance only did the fungus make any headway. The inner surface of the calyx of a single Goliath flower was seen to be covered with it about ten days after inoculation ; nevertheless, this flower set an excellent fruit. It is not believed, therefore, that the " running off " of Lee's is due to attack by *C. herbarum*. As to other species of fungi, if present, disinfection trials were made to eliminate their possible effect. Before coming into flower the Lee's in the glasshouse were treated twice with Bordeaux Mixture, Lime Sulphur or Uspulun. After selfing, the Lee's again set no fruit, but when crossed with Goliath 39% of the flowers produced fruit. Disinfection therefore did not improve the setting of Lee's, and its failure is not believed to be due to any fungus attack.

(5) *Soil conditions.*

It is known that a dry soil induces fruit dropping, and water was therefore deliberately withheld from some of the plants in the glasshouse before the opening of the flowers. As a result the flower buds withered and dropped unopened, but this in no way resembled " running off ", i.e. the dropping of flowers and unripe fruits. Water was also withheld just after the fruit had set, but the fruits did not drop ; they ripened without reaching full size and remained attached to the stalks.

To ascertain whether nutrition was at fault, five plants were watered once or twice a week, starting before the flowering period and continuing for some weeks afterwards, with dilute Wagner's nutrient solution (18). They showed an improved leaf colour as compared with the untreated controls, but the selfed flowers still set no fruit, though those crossed set a rather larger number than the controls.

Soil acidity was also investigated. Two plants were grown in soil adjusted to a pH of 7 to 8, three others in one of pH 4 to 5. In both, the selfed flowers

set no fruits; when crossed, 50% set in the alkaline and 42% in the acid soil. The figures do not point to any marked influence of soil reaction.

(6) *Reversion.*

This virus disease causes severe losses in yield. In the Belgian plantation very little Reversion was evident, but since it might have been latent there ten Lee's B scions were grafted in the spring of 1935 on two Goliath plants in pots, and ten healthy Goliath scions on Lee's B stocks. No symptoms appeared on any of the plants during 1935 or 1936, hence Reversion cannot be the cause of Lee's unfruitfulness.

(7) *Cytology.*

Since Crane and Lawrence (7) have shown that polyploidy is an important factor in causing sterility, the number of chromosomes was determined in Lee's, Lee's Prolific from East Malling, Goliath, Boskoop, Wellington, Naples Black, Daniel's September and Sivergieter's Black. In no case was the diploid number sixteen found to be exceeded. Polyploidy, therefore, is not the cause of fruit failing to set in Lee's.

(8) *Spring frosts.*

Undoubtedly spring frosts may cause serious damage to black currants, and the effects of this were carefully studied in the Belgian plantation. In 1935 damage occurred chiefly in Goliath, in 1936 in Lee's, which blooms somewhat earlier. Both varieties showed the same symptoms, viz. shrivelling and subsequent desiccation of the floral organs and shrinking of the ovary, the ovules drying up and becoming brown. The flowers afterwards dropped in a completely shrivelled condition, quite different from that seen in "running off".

(9) *High temperature.*

High temperature during the flowering period sometimes causes "running off" in Ribes, but it is usually the terminal flowers on the racemes that open in the warmest weather, and fail to set fruit. In Lee's there is no such tendency, nor did temperatures somewhat higher than normal injure the flowers.

IV. MICROSCOPICAL INVESTIGATION.

As a result of the experimental work described above it was clear that the importance of foreign pollen for Lee's flowers was paramount above all other factors. Hence the processes of pollination and fertilization were subjected to microscopical study. The ovaries, in different stages of development, were fixed in Flemming's Solution and embedded in paraffin. Sections were cut and stained with either iron-haematoxylin or cotton blue. It was first thought that Lee's pollen tubes might not grow down Lee's styles, or at any rate too slowly to reach the ovules in time to effect fertilization. The tubes of

pollen from different sources were therefore studied in Lee's styles, and it was found that in both selfed and crossed flowers the tubes reached the ovaries on the second day after application to the stigma.

Following the lines indicated by Asami (2) and Yasuda (20) the influence of the ovaries was studied, and it was found that the presence of Lee's ovaries was of no consequence. In cut styles, whether from Lee's or Goliath flowers, the tubes made headway as rapidly when put on a Lee's as on a Goliath ovary or when left in moist air not in contact with any ovary. Thus, it may be concluded that the failure to set fruit in selfed Lee's is not due to any retarding influence on its pollen tubes exerted by its own stylar tissue or ovary.

Fertilization must be inhibited, therefore, at a later stage, viz. during the course of the tube through the ovary or at the moment of entering the micropyle. On the other hand, the embryo may die soon after fertilization has occurred.

Selfed and crossed flowers that had previously been emasculated were fixed at intervals after artificial pollination. Non-pollinated Lee's flowers were also fixed. It was thus possible to compare the course of events in normal setting with that ensuing when fertilization does not occur.

If "running off" is due to the failure of the pollen tubes to reach the ovule or of the male nuclei to fuse with the female ones, the sections would show no differences between the ovules in emasculated and non-pollinated Lee's or Goliath flowers and those in Lee's flowers artificially pollinated with Lee's pollen. If, on the other hand, fertilization apparently occurred, and a short-lived embryo was produced, the first stages after selfing would be similar to those following cross pollination, they would differ only later on, i.e. about fourteen days after pollination, when dropping was beginning. The results obtained were as follows:—

Emasculated Lee's flowers, not pollinated.—At the start the ovules appear quite normal, and the different nuclei in the embryo sac can be distinguished (Fig. 5). After 8 to 12 days the ovules begin to shrivel, the inner integument separates from the outer although the embryo sac is still normal; at any rate the nuclei appear unchanged (Fig. 6). Beyond 12 days the embryo sac can no longer be distinguished, the contents of the ovule shrivel and degenerate (Fig. 11).

Emasculated Lee's flowers crossed with Goliath pollen.—A difference between the ovules that will develop into seeds and those that appear not to have been fertilized can be seen at least 5 days after pollination. The former increase considerably in size, the latter do not. After about 7 days these unfertilized ovules begin to shrivel, the inner integument separates from the outer, the volume of the embryo sac being thus diminished. The nuclei, however, remain visible for a few days longer. If an ample supply of Goliath pollen has been provided, these unfertilized ovules are soon pushed aside by

the swollen fertilized ones, the size of which has increased considerably by about 9 days after pollination. At this time, also, the embryo makes its appearance (Figs. 7 and 8). Later stages of embryos, about the 19th day, may be seen in Fig. 9. If only a very small number, such as five, of Goliath pollen grains have been applied, fewer ovules are pushed aside ; nevertheless these degenerate as described above. Hence it may be assumed that lack of pollen is the cause of degeneration in both cases.

Emasculated Lee's flowers selfed.—The development of the ovules in selfed Lee's is essentially the same as that in crossed flowers, but the number of ovules that swell is much less and they only very slightly push the unfertilized ones aside. The ovaries resemble those described above from flowers that received only very few Goliath pollen grains. (Compare Figs. 10 and 11.) The following figures for swollen ovules were obtained when ample supplies of both pollens were used :—

Days after pollination.	Goliath Pollen.	Lee's Pollen.
5	0	0
9	5–19	0–2
15	5–20	0–2
19	9–15	1–2 (3)

No " running off " occurred in this case until 9 days after pollination ; the minimum number of days before "running off " started in other experiments was usually 7. The time is probably dependent on temperature and prevailing wind. The following observations hold good for both selfed and crossed flowers of Lee's :—

(a) The embryo is visible in swollen ovules only ;

(b) A swollen ovule has never been observed to shrivel later on.

The critical moment must therefore lie before the ovule swells. Swollen ovules become seeds, and because an embryo can be detected only in swollen ovules it must be concluded that degeneration begins before an embryo is formed. In other words, the ovules shrivel because fertilization does not occur or the shrivelling begins immediately after nuclear fusion.

The microscopical preparations were compared with others made of " run off " flowers collected in the Belgian plantation in 1935 as well as from the experimental plants in that year and in 1936. The number of swollen ovules in " run off " fruits was, on the average, less than 1 (on a single occasion 3 were noted) whilst the fruits that remained attached until after June 6th contained an average of 12. The remainder had shrivelled in exactly the same way as in the experiments described above. The condition greatly resembles that of selfed flowers seven or more days after pollination. Such selfed flowers began to drop at least a week after pollination. Since the flowers in the plantation

were observed to drop about fourteen days after blooming, roughly speaking, the facts are concordant. The opinion that "running off" is due to lack of foreign pollen is thus confirmed by this comparison with selfed flowers. The conclusions to be drawn from the observations made are as follows:—

(1) Failure to fertilize is not due to insufficient growth in length of the pollen tubes.
(2) It is not connected with the formation of an embryo, which, being non-viable, afterwards degenerates.
(3) It may result from the failure of the pollen tube to penetrate into the ovule or the failure of the male and female nuclei to fuse.

Since neither of these stages has been met with in the preparations made, it has not been possible to determine the exact point at which the fertilizing process goes wrong.

V. Observations in the Plantation.

A careful watch was kept for any pests or diseases that might be responsible for defective fruit setting. In the spring of 1935 and of 1936 damage due to *Incurvaria capitella* was noted, but it was confined to the destruction of unopened winter buds. No other insects were noted. "Big bud" also occurred in the plantation, but its extent was not serious. Reversion was also seen, but chiefly in the varieties other than Lee's. The fungus *Stereum purpurem* was observed causing silvering of the leaves and killing many branches in the summer. On these dead branches its fructifications developed in the autumn.

In 1935 typical and severe "running off" occurred but it was less serious in 1936. This may be explained by the circumstance that in the latter year spring frosts injured Lee's to such a degree that the number of Lee's flowers remaining, in proportion to the quantity of Goliath pollen available, was more favourable than in the previous year. In order to check this supposition and to determine the approximate number of flowers and buds killed by frost, the original number of buds was counted on a few branches remote from each other and also the number of flowers that had opened or were likely to do so. In three out of four cases Lee's and Goliath branches were compared. The percentage of frost-killed flowers in Lee's was found to be 82, in Goliath 42. The percentage set of fruit of the undamaged flowers was 40 in Lee's and 75 in Goliath when examined on May 26th, 1936.

Wellington, Hatton and Amos (19) have pointed out that the visits of bees to black currant flowers are favoured by sunshine and shelter, and it was therefore expected that weather conditions, particularly wind and cloudiness, might be connected with "running off". Hence the attempt was made to follow the flowering and fruit setting on certain branches of Lee's by recording weekly the newly opened flowers and afterwards noting which of them had set fruit.

Unfortunately spring frosts interfered with the observations, hence the number of flowers recorded was much smaller than had been intended. Observations were also made on cloudiness and wind in the neighbourhood of the plantation during the period. The receptivity of the flowers was assumed to extend for both five and seven days. In both cases the results were the same, viz. the setting of the fruit was considerably better during the periods when the weather was favourable to bees—sunny or mainly sunny with slight wind only—than when it was unfavourable to them, and this supports the view that the "running off" in this plantation was due to lack of cross pollination.

The average berry weight and seed content was also determined for Lee's surrounded by and also remote from Goliath bushes. The average berry weight of the former was 0·73 gm. and the average number of seeds 19. In the latter, the berry weight was 0·57 gm. and the seeds numbered 9. In Goliath berries under similar conditions the average numbers of seeds were 23 and 25 respectively. From these results it is fair to conclude that the amount of available Goliath pollen was decisive for the fertilization of the Lee's ovules and the setting of the fruit.

SUMMARY AND CONCLUSIONS.

1. The variety of black currant known on the Continent as Lee's is not identical with the "Lee's Prolific" of English pomological literature. Its exact identity has not yet been established.

2. This variety is to a high degree self-unfruitful, and not very productive even when crossed.

3. Its pollen proved to be perfectly normal and viable; its ovules also have a normal appearance.

4. Its unfruitfulness is manifested in the insignificant number of fruits set and their low individual weight, when not crossed by foreign pollen, e.g. that of Goliath. In the absence of such pollen the typical behaviour is a heavy drop of fruit within a week or so after flowering. In the present paper this is designated as "running off".

5. One particular fungus (*Cladosporium herbarum*) was proved to have no connection with "running off", and disinfection against the possible presence of others did not prevent it. The defect was not connected with soil factors (such as abnormal pH, insufficient nutrition and drought), Reversion, spring frosts or high temperature. Polyploidy was not detected.

6. The pollen tubes reached the ovary successfully, and degeneration of embryos did not occur. The cause of failure appeared to lie in the failure of the pollen tube to penetrate into the ovule or the failure of the male and female nuclei to fuse.

7. Observations made on a plantation in Belgium, mainly consisting of Lee's, taken in conjunction with the results of the investigations carried out, point to the necessity of ensuring adequate cross pollination by regularly and closely interplanting this variety with others (such as Goliath) if a reasonable set of fruit is to be secured.

LITERATURE REFERENCES.

(1) *Amos. J.* Annual Report, East Malling Research Station, 1928, 1929 and 1930, II Supplement, 1931.
(2) *Asami, Y.* Proc. Amer. Soc. Hort. Sci., 23, 1926.
(3) *Bennet, F. T.* Ann. Appl. Biol., 15, 1928.
(4) Verslag v.d. Proeftuin, Breda, 1926-7.
(5) *Bunyard, E. A.* Handbook of Hardy Fruits, II, London, 1925.
(6) *Crane, M. B.* and *Lawrence, W. J. C.* Journ. Pom. & Hort. Sci., 7, 1929.
(7) ———. The Genetics of Garden Plants, London, 1934.
(8) *Darlington, C. D.* Journ. Pom. & Hort. Sci., 6, 1927.
(9) *Dearness, J.* and *Foster, W. R.* Canad. Journ. Res., 9, 1933.
(10) Deutschlands Obstsorten, Stuttgart.
(11) East Malling Research Station Ann. Reports from 1923 onwards.
(12) *Hatton, R. G.* and *Amos, J.* Gardeners' Chronicle, 61, 1917.
(13) *Hogg, R.* The Fruit Manual, 4th Edition, London, 1875.
(14) *Kearney, Th. H.* and *Harrison, G. J.* Journ. Agr. Res., 44, 1932.
(15) Long Ashton (Univ. of Bristol) Ann. Reports from 1918 onwards.
(16) *Ridler, W. F. F.* Ann. Appl. Biol., 11, 1924.
(17) *Tydeman, H. M.* Journ. Pom. & Hort Sci., 8, 1930.
(18) *Wagner, P.* Die Ernährung gärtnerischer Kulturpflanzen, Berlin, 1908.
(19) *Wellington, R., Hatton, R. G.* and *Amos, J.* Journ. Pom. & Hort. Sci., 2, 1921.
(20) *Yasuda, S.* Bull. Imp. Coll. Agri. and For. Morioka, 20, 1934.

(*Received* 6/4/37.)

FIG. 1.

Left plant: Ninety-seven "Lee's" flowers selfed; yielded no berries.
Right plant: Ninety-eight "Lee's" flowers crossed with Goliath; yielded thirty-three berries.

FIG. 2.

Top: "Lee's" branch, the flowers of which have been crossed with Goliath. Bottom: Ditto; flowers selfed.

FIG. 3.

From top to bottom: Three "Lee's" branches crossed with Goliath. Fourth branch "Lee's" selfed. Fifth branch "Lee's" insect-pollinated.

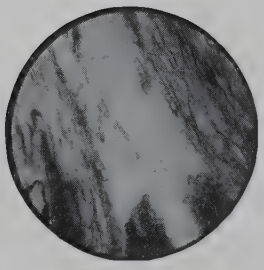

FIG. 4.

Pollen tubes reaching the ovary of a selfed "Lee's" flower.

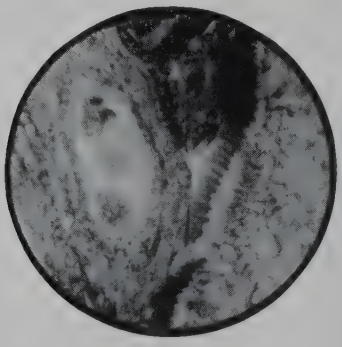

FIG. 5.

Unchanged embryo-sac in emasculated "Lee's" flower.

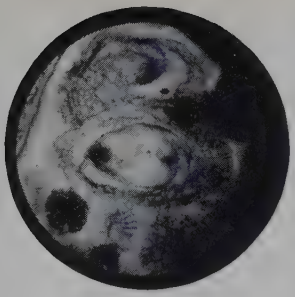

FIG. 6.

Inner integument retreating, eight days after emasculating.

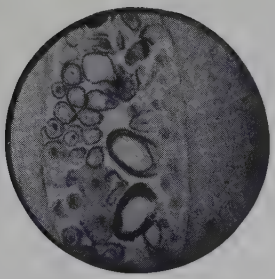

FIG. 7.

Ovary of crossed "Lee's" flower, nine days after pollination.

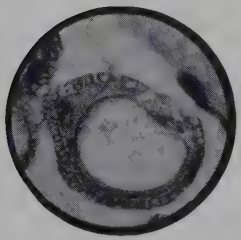

FIG. 8.

Ovule of crossed "Lee's" flower, nine days after pollination. Early stage of embryo development.

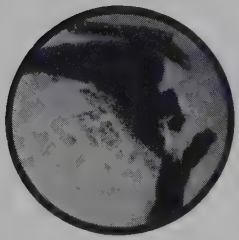

FIG. 9.

Embryo development nineteen days after cross-pollination.

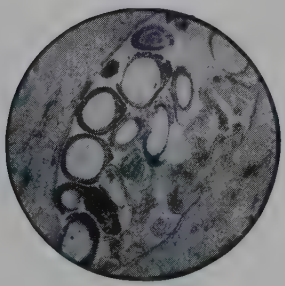

FIG. 10.

Shrivelled ovules pushed aside by swollen ones thirteen days after cross-pollinating "Lee's" flower.

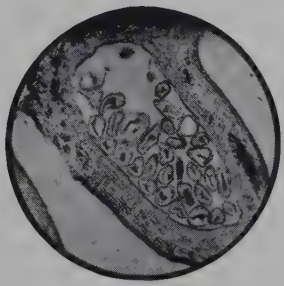

FIG. 11.

Shrivelled ovules thirteen days after selfing.

OBSERVATIONS ON THE INCIDENCE OF DOWNY MILDEW ON NEW SEEDLING VARIETIES OF HOPS AT EAST MALLING, 1924-36

By F. H. BEARD,
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Introduction.

A considerable part of the hop research carried out at the East Malling Research Station has consisted of the growing on, and observation of the behaviour of, new seedling varieties raised by Professor E. S. Salmon at the South-Eastern Agricultural College, Wye. Separate Reports by Professor Salmon on this work have been published annually by the Station.

The seedlings are grown in rows of from 15-18 hills each (a few in the earlier years, 30-32 hills) and are trained on the "Butcher" system with the top wire 13 ft. 6 in. high. The alleys are 7 ft. wide, and in about two-thirds of the garden the hills are 7 ft. apart in the rows, giving 889 hills per acre, whilst in the remaining portion the hills are 6 ft. apart in the rows, giving 1,037 hills per acre. The manurial and cultural operations have been uniform over the whole garden, but the type and quantity of manures applied have varied from year to year. Details of the manuring for each season are given in the Reports mentioned above.

Whilst the aroma of the best English varieties is very good, their preservative value is somewhat lower than that of the best Continental hops and very considerably below that of the choicest American sorts, which have a very strong aroma. The native American hop (*Humulus Americanus*) is distinct from the European hop (*Humulus Lupulus*) from which English and Continental varieties have been derived (1) hence seedlings raised from American hops crossed with English male hops are true hybrids. To obtain new varieties combining the good qualities of both, Professor Salmon has crossed Continental, American, and wild hops from New Mexico and Canada with English male hops, and the main object of the trials at East Malling has been to determine the relative cropping capacities of the seedlings and to provide material for chemical and brewing tests. However, the hop Downy Mildew (*Pseudoperonospora Humuli*) made its first appearance in this country in 1920 and spread rapidly from 1924 onwards, hence observations have been made on the incidence of this disease on the new seedlings.

The disease has been described by Salmon and Ware (6) and it is not necessary to do more here than note briefly the various forms in which it

manifests itself. Early in the season stunted shoots known as "basal spikes" arise from the hills. On these, under damp conditions, spores are produced which cause infection of the leaves of normal bines and ultimately of the burr and cones. Moreover, during the course of the season the tips of the growing bines and the young laterals may be attacked and "terminal" and "lateral spikes" may arise. Finally, under certain conditions, the fungus may kill the bases of the bines during the dormant season, and in certain varieties, indeed, the entire rootstock. The course and intensity of Downy Mildew attacks during a given season is governed (apart from varietal resistance or susceptibility) almost entirely by weather conditions, being negligible or slight in a dry season, but devastating in a wet one unless the "spikes" are removed and the bine sprayed with Bordeaux mixture.

At East Malling, records have been taken at intervals throughout the growing season on the number of hills of each seedling showing spikes. Unfortunately it has not been possible to count the number removed from each hill, although those seedlings showing many spikes per hill have been noted. Thus, whilst the records give a reasonably accurate indication of those seedlings not prone to show this form of the disease, those with all hills showing a moderate number of spikes cannot be differentiated from those having all hills attacked, but with perhaps only one spike per hill. In certain seasons the cones have become attacked by picking time, and notes have been made on the presence or absence of cone infection of the seedling as a whole and not upon individual hills. In the earlier years all spikes were removed at frequent intervals during the season but no spraying was done. In more recent years the whole experimental garden has been sprayed with Bordeaux mixture (10 lb. Copper Sulphate, 15 lb. hydrated lime, 100 gals. water) as a rule twice during the season. This has largely prevented attack of the cones, and has resulted in healthy crops from most of the seedlings even in seasons favourable to the disease. In a mixed garden of some 300 very early to very late varieties, planted at random in small plots, it is naturally impossible to spray at the optimum time for each and every seedling. Those seedlings with only a moderate or slight amount of bine (particularly of "heads" over the top wire) at the time of spraying will be more copiously covered with the mixture than those having a heavy growth of bine. This difference in cover is greater when application is by "hop washer" than when hand lances are employed. Both methods have been used on different occasions. Differences in intensity of attack on the cones therefore, may not always be due to any real differences in susceptibility to infection, but to one or both of the above factors.

The collection of seedlings has undergone constant changes, those showing little merit after a few years having been grubbed and replaced by fresh selections. Very few have been in the garden over the whole period, 1924-36, so that for

many of them records of cone infection are not available over both sprayed and unsprayed periods and for both good and bad seasons. Thus records of cone infection can give only a very rough idea of the susceptibility of the seedlings. Spikes arise in most seasons long before the first spraying (mid July) and the records are therefore a fairly accurate measure of the tendency of the seedlings to show the disease in this form. In some years (e.g. in 1936) lateral spikes are formed late in the season, and burr and young cones may be attacked. Such late infection will of course be influenced by spraying, as is also the infection of the ripe cones.

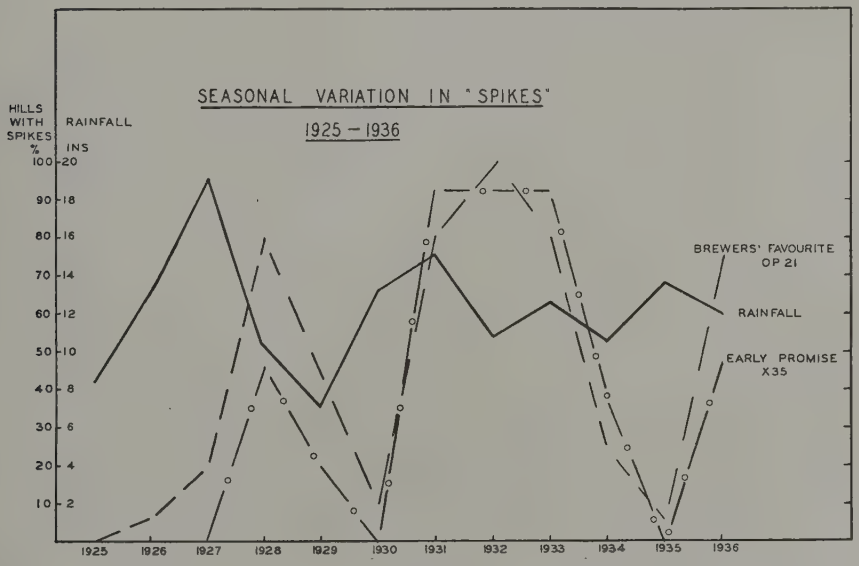

Fig. 1.

Seasonal Variation.

There has been very considerable seasonal variation both in the severity of attack and in the form of infection most prevalent. The former is illustrated in Fig. 1, which shows for two seedlings, Brewers' Favourite (OP21) and Early Promise (X35), the percentage of hills* showing spikes in each season from 1925-36. These seedlings have been growing in the garden over the whole period, but others show a similar rise and fall in the severity of attack.

* Early Promise, 15 hills recorded through the whole period. Brewers' Favourite, 32 hills recorded 1925-30, 16 hills 1931-35, 140 hills 1936. "Brewer's Favourite" = (Oregon Cluster × English Male) × English Male. "Early Promise" = Hop of unknown origin × English Male. Rainfall, April-September inclusive.

Particulars of the occurrence of the disease every year over the whole country have already been published (2, 3, 4, 5, 7, 8, 9, 10) but it did not appear at East Malling until 1924 and the main features of each season's attack there are as follows:—

1924. No basal, lateral or terminal spikes observed; attack on leaves of plants in nursery beds and on leaves and cones of some seedlings in hop garden.

1925. Both basal and terminal spikes occurred, reaching a maximum during July. Cones of some seedlings again attacked.

1926. A few spikes occurred, being most numerous during June. Certain seedlings again attacked on the cones.

1927. Spikes not very prevalent and reached their maximum by May 3rd. Many seedlings severely attacked on cones, some so badly that the crop was useless.

1928. Spikes reached a maximum at the end of July. Several seedlings were sprayed for the first time, but the cones picked from both sprayed and unsprayed were entirely free from the disease.

1929. Basal and terminal spikes not so common as in 1928, being most numerous about May 27th. Slight attack on the cones of the most susceptible seedlings.

1930. Spikes not so numerous as in two previous seasons, being commonest during the first half of June. Seedlings found susceptible to cone infection in earlier years sprayed on August 22nd. A number of seedlings, mainly unsprayed ones, were attacked on the cones.

1931. Spikes occurred very plentifully, reaching a maximum during June and early July. Two sprayings (July 15th and August 12th) protected the cones of all seedlings except those with an excessive amount of bine, many of which were attacked on the "heads".

1932. Spikes extremely prevalent, a special feature being the large number of lateral spikes on the lower half of the bine at the end of June and beginning of July. Terminal spikes also numerous during June. The hops were sprayed twice (July 27th and August 10th) and the cones remained healthy in nearly all cases.

1933. Basal spikes not so prevalent as in the previous season. Terminal spikes in abundance, however, from May 24th to June 6th and at the latter date lateral spikes were also numerous on many seedlings. This was probably due to the fairly high rainfall (2·21 in.) during May. On June 19th an extremely severe hailstorm passed across the garden damaging all growing tips of bines and laterals and cutting the leaves to shreds. In consequence of this much new lateral growth was produced, and this proved very susceptible to attack, encouraged by the

heavy July rainfall (3·18 in.). Two sprayings (three for very late seedlings) were given and all the cones were picked free from disease.

1934. Few basal or terminal spikes. Bordeaux mixture was applied on July 18th and August 9th, and there was no attack on the cones.

1935. Spikes were rare and there was no infection of the cones. Two sprayings were given.

1936. Hardly any basal spikes, but the very wet weather at the end of June and during July caused a very serious outbreak of the disease during the burr period. Three sprayings were given over the whole garden, and the late seedlings received an additional application. With only a few exceptions, the crop was gathered free from disease.

Incidence of Downy Mildew in Relation to Rainfall.

As the summer spores of the fungus require a film of water for their germination (2) a close correlation might be expected between rainfall and the severity of the disease, but it will be seen from Fig. 1 that there is little correlation between the severity of the disease on the two seedlings Brewers' Favourite and Early Promise and the total rainfall from April to September inclusive. There is, however, an apparent correlation between the rainfall of the previous summer and the development of spikes in the years 1926-31, though, with the exception of the season 1927-8, this is more apparent than real. This apparent lack of correlation can be explained with the aid of the monthly rainfall figures given in Table I. It will be noticed that there is great fluctuation in the rainfall from month to month, and that even in a wet season like 1927 some months may have a rainfall well below normal. Table I also includes the number of days on which rain was recorded in each month, since a large number of wet days, each with only slight rain, is likely to favour the spread of the disease more than a smaller number of wet days with a greater total rainfall. In most cases a high monthly rainfall is also associated with a large number of wet days, but there are certain exceptions. For example, September, 1933, had a high rainfall, but actually one day less on which rain fell than the same month in 1931, which had only about half the total rainfall.

In considering the incidence of the disease in relation to the rainfall, it will be more convenient to deal separately with the spike form of the disease and infection of the cones. Although spikes occurred in 1925 and 1926 they were only few in number. In 1927 they were more numerous, but not so plentiful as would be expected from the extremely heavy rainfall (over 19 in.) from April to September. It will be seen from Table I that April and May were very dry months and that the wet period did not begin until June. Evidently the fungus did not become active again in time to produce many spikes, but was able to cause a very severe attack on the cones.

TABLE I.

Summer Rainfall, 1924-36. East Malling.

Month.	No. of days on which rain fell.*												
	1924.	1925.	1926.	1927.	1928.	1929.	1930.	1931.	1932.	1933.	1934.	1935.	1936.
April ..	10	18	20	13	16	13	16	21	22	7	15	21	9
May ..	14	18	17	8	14	12	18	13	24	18	8	13	7
June ..	7	4	16	18	15	12	6	13	5	11	6	19	21
July ..	8	16	14	22	7	8	11	15	13	14	9	5	22
August ..	15	15	11	22	19	8	16	19	8	9	12	9	12
September ..	19	20	13	19	9	5	23	15	20	14	9	10	20
Total ..	73	91	91	102	80	58	90	96	92	73	59	87	91

Month.	Total Rainfall in inches.												
	1924.	1925.	1926.	1927.	1928.	1929.	1930.	1931.	1932.	1933.	1934.	1935.	1936.
April ..	3·31	2·01	4·77	1·58	2·01	1·17	1·28	3·94	1·81	0·85	2·87	3·31	1·31
May ..	2·21	2·01	1·86	0·84	2·00	1·34	2·32	1·99	3·06	2·21	0·71	1·82	0·44
June	2·03	0·28	2·64	3·73	2·40	0·98	0·50	1·32	0·69	2·01	1·48	1·63	3·95
July ..	2·99	0·35	1·71	3·96	1·58	1·04	2·16	2·41	2·12	3·18	2·02	0·94	2·80
August ..	1·91	1·79	1·32	4·57	2·25	2·19	3·64	3·42	1·26	0·69	1·83	2.67	1·20
September	3·75	1·80	0·67	4·76	0·34	0·61	3·30	1·94	1·97	3·56	1·38	3·57	2·34
Total ..	16·20	8·24	12·97	19·44	10·58	7·33	13·20	15·02	10·91	12·50	10·29	13·94	12·04

Month.	Mean Rainfall at East Malling 21 years.
April	2·14
May	1·66
June	1·53
July	2·21
August	2·14
September	2·14
Total	11·82

* Including those days when rain was observed, but the amount was too small to be measured (i.e. less than ·01 in.)

The great abundance of spikes in 1928, as shown in Fig. 1, can possibly be attributed to the extremely heavy rainfall during August and September in the previous year, and to the fact that no spraying was done in that season. On the view that heavy rainfall may wash numbers of spores to the ground and thus facilitate infection of the buds on the hills, an explanation is found for the great prevalence of spikes in 1928. Whilst the rainfall for 1928 would not account for the increase in the number of spikes over the previous season, the months of April, May and June were each slightly more rainy than normal and enabled the fungus to continue to spread, until checked by a dry July.

The number of spikes formed was less in both 1929 and 1930. The summer of the former year being extremely dry, the decrease was to be expected, but the summer rainfall of 1930 was above normal. This, however, came too late (August and September) to cause the formation of spikes.

It will be noticed that prevalence of spikes was very great in 1931-3 inclusive. Whilst both 1931 and 1933 had a rainfall above normal, that for 1932 was about an inch under the normal for the six months ; but in this year, May, the month when many shoots are coming from the hill, was exceptionally wet, whilst April had a large number of days on which rain fell. There was a large reduction in the numbers of spikes in 1934 and 1935, the reduction being greater in the latter season. The rainfall for 1934 was below normal, whilst in 1935, although April and September were wet, the intervening months were relatively dry.

In 1936 both April and May were dry and there were very few basal spikes ; June and July were rainy, however, and there was a great development of lateral spikes amongst the burr in the latter month.

As to the incidence of the disease on the cones, whilst the attack on those of certain seedlings in 1924 may be attributed to the heavy September rainfall, that of 1925 and 1926 must be considered as due to the susceptibility of the seedlings concerned and to the absence of spraying. As was to be expected from the very heavy rainfall in 1927 and the absence of spraying, the attack on the cones was extremely severe.

Cone infection was absent or only slight in the seasons 1928, 1929, 1932, 1933, 1934, 1935, 1936. Whilst the seasons 1928, 1929, 1932, 1934 were dry during August and September, in 1933 and 1935 September was wet, but the rainfall did not occur until towards the end of the month, so that the crop was picked before the fungus had time to re-establish itself after a quiescent period. In 1936 the absence of diseased cones can be attributed to a dry August followed by a September rainfall only just above normal.

The disease was present on the cones to a considerable extent on certain seedlings in 1930 and 1931. In the former year both August and September were wet, and in the latter, August only. From 1931 onwards the hop garden

has been sprayed with Bordeaux mixture at least twice each season, and this has prevented attack of the cones of all except the most susceptible seedlings.

It should be pointed out that many of the seedlings are extremely susceptible to cone infection and are likely to be attacked even in moderately dry seasons, unless sprayed. In unfavourable seasons they require more than two applications to secure a healthy crop. It is these very susceptible seedlings that have indicated the seasons mentioned above which favoured cone infection.

Relative Susceptibility of Seedlings of Various Parentages.

The number of hills in the rows of the several seedlings has not been uniform, nor has the number of hills of any one seedling been constant from year to year. It is therefore necessary to express the number of hills showing spikes as a percentage of the total number of hills of the particular seedling in order to compare the figures obtained for the different seedlings. Owing to the fact that most of the seedlings have proved to be carriers of Mosaic, to which true Goldings and Golding varieties are highly susceptible, it has been necessary to eliminate the latter from the garden and also any seedlings that have proved susceptible to this disease. The only commercial variety in the Research Station garden for comparison with the new seedling varieties is Fuggle, which shows no symptoms of Mosaic and is considerably more resistant to Downy Mildew than Goldings and Golding varieties, which have proved to be, in wet seasons, very readily attacked on both bine and cone. In the earlier years, Goldings were grown, but the incidence of Mosaic rendered Downy Mildew records of little value.

Table II shows the incidence of bine and rootstock infection in the seedlings in the several parentage groups.

The figures are based on the severest attack on each seedling over the period during which it has been in the garden. In 1936 many seedlings showed a large number of lateral spikes amongst the burr, but as this occurred late in the season, it was probably influenced by the spraying which was then taking place ; it must be noted also that it took a certain time to record and remove these spikes, and a period of ten days elapsed between the making of records concerning the first and the last seedlings in the garden. The figures for 1936 have not therefore been used in compiling the Table. Seedlings planted out after 1931 have not been included in this survey, as the years 1934-6 have shown but little spike infection.

Late Bavarian × English male hop.

The late Bavarian variety was not named, but is believed to be allied to Hallertau, one which has proved to be very susceptible to Downy Mildew on the Continent. Out of a total of fourteen seedlings, eleven have proved highly

TABLE II.

Incidence of Bine and Rootstock Infection.

Parentage of Group.	No. in Group.	Number of Seedlings in each percentage grade of hills showing spikes.										Seedlings with hills killed.	Seedlings with strap-cuts only killed.
		91% to 100%	81% to 90%	71% to 80%	61% to 70%	51% to 60%	41% to 50%	31% to 40%	21% to 30%	11% to 20%	10% and under.		
Late Bavarian × English male	14	11	1	1	1	—	—	—	—	—	—	2	—
Late German Variety (260-1) × English male	17	12	—	3	1	1	—	—	—	—	—	—	
German Variety "Elsass" × English male	4	3	—	—	—	—	1	—	—	—	—	—	—
(Saaz × English male) × English male ..	11	2	3	1	1	2	2	—	—	—	—	—	—
Seedlings of New Mexican Hop	27	26	1	—	—	—	—	—	—	—	—	—	—
Seedlings of Y90 (New Mexican Seedling)	8	5	—	2	—	—	1	—	—	—	—	-	—
Seedlings of Wild Hop, Manitoba ..	49	31	4	5	5	1	3	—	—	—	—	2	4
Oregon Cluster × English male	6	3	1	1	—	1	—	—	—	—	—	6	—
Seedlings of M45 (Oregon Cluster × English male)	31	9	7	5	3	3	2	—	1	1	—	14	2
Seedlings of OP13 (Seedling of M45) ..	25	11	4	1	3	3	—	1	—	1	1	11	—
(Oregon Cluster × English male) × English male, other than seedlings of M45 ..	20	17	1	1	1	—	—	—	—	—	—	4	—
Tolhurst × English male	7	2	—	1	2	—	—	—	—	2	—	—	—
Seedlings of Golden Hop	16	6	4	2	1	2	—	1	—	—	—	—	—
Seedlings of Hops of Unknown Origin ..	14	7	—	2	3	—	1	—	—	—	1	—	—
Strains of Commercial Variety, Fuggle ..	12	—	—	—	1	1	1	4	3	—	2	—	—

susceptible to attacks on the bine, with over 90% of the hills showing basal spikes in bad years. Three seedlings have been only slightly less severely attacked, having from 61% to 90% of the hills with spikes. These seedlings have, in certain seasons, shown a considerable amount of the angular spot form of the disease on the lower leaves. As well as having a large number of hills showing spikes, these seedlings have also had a large number of spikes per hill in seasons favourable to the disease.

Six seedlings have proved very susceptible to cone infection when not sprayed. Six of the eight seedlings that have not shown any cone infection have been in the garden only since routine spraying has been adopted. Two seedlings have suffered from infection of the rootstock and strap-cuts, but not to a serious extent.

Late German variety (260-1) × English male hop.

The late German variety (260-1) was imported for breeding work at Wye in 1902, and, owing to its richness in soft resins, was used as the female parent in a number of crosses. As the name of the variety is unknown, it is not possible to state its susceptibility to Downy Mildew when grown in its native land.

Out of seventeen seedlings, twelve have had over 90% of the hills showing spikes, whilst three have shown only slightly less severe an attack with over 70% of the hills affected ; two others have had an infection of between 50% and 70%. These seedlings are very similar to those of late Bavarian parentage as regards angular spotting on the lower leaves and the large number of spikes per hill.

Ten seedlings have been severely attacked on the cones when unsprayed. The remaining seven which have not shown infection of the cones, were not established in the garden before spraying was adopted.

German variety Elsass × English male.

Elsass is susceptible to Downy Mildew when grown in Germany. Only four seedlings have been under trial, and of these three have proved very susceptible to the spike form of the disease with over 90% of the hills attacked, whilst one has shown itself fairly resistant, with 41%-50% of the hills attacked. The three which produced most spikes have also proved susceptible to cone attack when unsprayed.

(Saaz × English male) × English male.

Prior to 1931, Saaz had shown itself to be practically immune from Downy Mildew in its native district in Czechoslovakia, but in that year its resistance broke down (4). In this respect its behaviour was similar to that of Fuggle in this country. Only one seedling (P13) of the first generation from Saaz has

been grown in the Research Station garden; it has had 75% of the hills showing spikes and was badly attacked on the cones when not sprayed. However, eleven second generation seedlings of Saaz have been tested and these have shown a very even distribution as regards susceptibility to spikes, with from 41% to over 90% of the hills attacked.

Cone infection was recorded on nine seedlings in the earlier years before spraying was adopted. Neither of the two seedlings that have not shown cone infection was growing in the garden in the earlier years.

Seedlings of the New Mexican Hop (Humulus Americanus, *var. neo-mexicanus*).

All American cultivated varieties have proved very susceptible to Downy Mildew in their own country, but the reaction of *neo-mexicanus* to the fungus in its native country is unknown. Of a total of twenty-seven seedlings, twenty-six have had over 90% of the hills showing spikes, whilst the remaining seedling has had over 80%.

The seedlings appear to be particularly prone to produce lateral spikes on the first 5 ft. or so of the bine. Although the percentage of hills with spikes is high, the actual number of spikes per hill is usually decidedly less than that of seedlings of the late Bavarian and late German (260-1) crosses.

Fourteen seedlings have been attacked on the cones when unsprayed, and seven of these have shown cone infection even when sprayed. The thirteen seedlings that have not been attacked on the cones were established in the garden only after spraying became a routine measure.

Whilst the majority of these seedlings must be considered as highly susceptible to cone infection, it is doubtful if a few, such as "Cats-tails" (OZ79) and OI47, are much more susceptible than certain commercial varieties, such as Canterbury Golding. It is evident that clean crops of these seedlings can be obtained by prompt removal of all spikes combined with thorough spraying.

Seedlings of Y90 (Seedling of New Mexican Hop).

The seedling Y90 has proved very susceptible to infection of both bine and cones, the latter having been attacked when the hills were sprayed. Of eight seedlings so far tested, five have had over 90% of hills with spiked shoots, two have had 71-80%, and one has proved somewhat resistant to this form of the disease, with an infection of from 41-50%.

Two seedlings were attacked on the cones in 1931, a very wet summer, when only two sprayings were given. None of the seedlings was established in the garden when no spraying was done.

Seedlings of Wild Hop, Manitoba.

Of a total of forty-nine seedlings, thirty-one have proved very susceptible to infection of the bine, with over 90% of the hills bearing spiked shoots. The remainder showed a fairly even range of susceptibility with from 41% to 90% of the hills attacked.

Manitoba seedlings are liable to develop lateral spikes on the lower part of the bine, but to a rather less extent than the New Mexican seedlings.

Fifteen seedlings have been attacked on their cones, and thirteen of these even when sprayed. Of thirty-four seedlings that have not shown cone infection, ten were not established in the garden prior to spraying. Most of these seedlings make a very large amount of lateral growth late in the season, and therefore do not receive a thorough covering when sprayed.

The new variety, Brewers' Gold (C9a), of this parentage, which has in several seasons proved richer in preservative value than the best American hops, has, however, never been attacked on the cones at East Malling when sprayed. Two seedlings of this cross have had hills killed through the fungus entering the rootstock, and four seedlings have borne diseased strap-cuts.

Oregon Cluster × English male hop.

Only six seedlings have been under trial. Of these, three have had over 90% of the hills bearing spikes, and of the other three one has had an infection of over 80%, another of over 70% and the third of over 50%. One seedling has been severely attacked on the cones even after spraying, but the others have been free from any cone infection. Only one seedling was in the garden in the years before the adoption of spraying. All six seedlings have suffered severely from infection of the rootstock.

Seedlings of M45 (Oregon Cluster × English male).

The thirty-one seedlings have shown a fairly wide variation in the number of hills bearing spikes, but about half have had more than 80% of the hills attacked. Only two seedlings (OK14 and CC87) have shown considerable resistance, one with under 30% and the other with under 20% of spiked hills.

Prior to Bordeaux spraying, four seedlings were attacked on the cones. Of those that have not been attacked on the cones, four were not planted until after spraying was adopted. Out of the thirty-one seedlings, fourteen have had hills killed by the fungus, whilst two have had the strap-cuts killed. Included amongst those with hills killed is the seedling CC87 which suffered least (under 20%) from the spike form of the disease.

Seedlings of OP13 (Seedling of M45).

The twenty-five seedlings have shown a very similar range of susceptibility of the bine to that of the seedlings of M45. Three were not growing in the

garden in the years before spraying was adopted. Only one has shown cone infection, but this seedling (M35) is an early one and it is likely that spraying has normally been too late to protect the cones. The last application has often been made when M35 was in hop, and the immature cones perhaps already showing signs of infection. Hills of eleven seedlings have been killed by the fungus.

Seedlings of (Oregon Cluster × English male) × English male.

Included in this group are all the second generation of seedlings from Oregon Cluster, except those derived from M45 (Oregon Cluster × English male). Seedlings of this group have shown a greater incidence of spiked hills than those derived from M45. Of twenty seedlings, seventeen have had more than 90% of the hills showing spiked shoots, and none has had less than 60%.

Eleven seedlings have been attacked on the cones when not sprayed. Of the nine that have remained free from cone infection, three have been in the garden only since Bordeaux spraying became general.

Four seedlings have had hills killed by the disease, and three of these are seedlings of M52 (Oregon Cluster × English male).

Tolhurst × English male.

Tolhurst has proved very susceptible to Downy Mildew when grown in commercial gardens. Only seven seedlings raised from it have been under trial, and they have shown great differences in the incidence of the spike form of the disease. Two seedlings have had over 90% of hills showing spikes, three have had between 60% and 80%, whilst two seedlings have shown considerable resistance. One of these, L21, has had the very low figure of 12% of the hills attacked in a bad year, whilst during the four years 1933-6 inclusive, no spikes have been found on an experimental plot of about half an acre of this variety. The spikes from L21 have always been removed before they developed any spores. This seedling has also shown itself to be either immune from or highly resistant to attacks on the cones.

Three seedlings of Tolhurst parentage have, as might be expected, been attacked on the cones when not sprayed.

Seedlings of Golden Hop.

The Golden Hop is an ornamental variety with yellow leaves, probably of German origin, and is of no brewing value. It is, however, immune from attacks of the ordinary hop Mildew (*Sphaerotheca Humuli*), hence its use as a parent for new varieties.

Sixteen seedlings have been under trial, and of these six have had over 90% of hills showing spikes, a further six have had from 70% to 90%, three from 50% to 70%, and one between 30% and 40%.

No seedlings have been attacked on the cones, but none was planted in the gardens when spraying was not practised.

Seedlings of Hops of Unknown Origin.

These have been raised from several hops of unknown origin found growing in the Wye College gardens by Prof. Salmon when he began his breeding work. Of fourteen seedlings observed, half have had over 90% of hills bearing spikes, five have had from 60% to 80%, one has proved somewhat resistant, with between 40% and 50%, while one, P43, has shown very great resistance to the spike form of the disease, having had less than 10% of the hills affected.

Six seedlings (including P43) have been attacked on the cones when not sprayed. The infection of P43, however, was extremely slight and occurred only in the very wet season of 1927. It is interesting to note that the female parent (F1) of P43 was very prone to produce spikes when grown at the Station, as was also another seedling (X66) derived from it.

Fuggle.

Eleven strains of Fuggle* originally obtained from various growers in Kent, Worcester, Hereford and British Columbia, have been under trial. Whilst none of the strains has suffered severely from spikes, there has been considerable variation in the number of hills bearing spiked shoots in the several strains. The most severely affected strain (from Kent) has had between 60% and 70% of the hills attacked, whilst two strains (from Kent and Worcester) have had less than 10%.

Many experienced growers have always maintained that there are distinct strains of Fuggle in cultivation, and this view appears to be supported by the above behaviour. In addition, it may be mentioned that in a cultural trial at this Station, in which clonal Fuggle sets (originally obtained from three different sources in Kent) are being grown, one strain has proved more resistant to frost and has so far given heavier crops than the others.

Spores have never been noticed on the spikes collected from Fuggle hills at the Research Station. It must, however, be remembered that the spikes have always been removed very promptly, and spores would presumably have developed had the spikes been allowed to remain longer on the hills. The cones of Fuggle have never been attacked in the experimental garden, even when not sprayed. Prior to 1930 Fuggle, in commercial gardens, had appeared to be immune from attack on the cones, even in the severe outbreak of the disease in 1927. However, in 1930, cases were reported where Fuggle was severely attacked on the cones, and Salmon and Ware (3) considered that a possible explanation of this lack of resistance might be the occurrence of a new biologic

* Not of clonal origin.

form of the fungus capable of attacking Fuggle cones. The freedom from cone infection of the Research Station strains of Fuggle may, therefore, be due to the absence of this biologic form.

Infection of Rootstocks and Strap-cuts.

Diseased strap-cuts were first noticed at East Malling in the winter of 1928-9, on two seedlings. The cuts showed brown discoloured patches on the outside, and when cut open were found to be discoloured inside also. The dormant buds on affected strap-cuts are brown instead of a normal healthy white colour. It was not until the winter of 1931-2 that the presence of the disease in the strap-cuts and hills of commercial gardens was reported by Salmon and Ware, although hills in gardens in France were reported to have been killed in 1926 (5).

Since the winter of 1928-9 infected strap-cuts have been found on various seedlings at cutting time each season, although the severity of attack has varied from year to year. In many cases the mycelium of the fungus has penetrated and killed the rootstock.

Forty-one seedlings have had their strap-cuts infected and hills killed by the fungus. Of this number, no less than thirty-five are descended from Oregon Cluster. All six of the seedlings of Oregon Cluster × English male have been severely attacked in strap-cuts and hills. Fourteen out of thirty-one seedlings of M45 (Oregon Cluster × English male) have been attacked, and eleven out of twenty-five seedlings of OP13 (a seedling of M45) have shown also infection of rootstock and strap-cuts. Of twenty seedlings of the second generation from Oregon Cluster (excluding seedlings of M45) four have proved susceptible to rootstock infection, and three of these are derived from the seedling M52 (Oregon Cluster × English male). A few other seedlings have also been attacked, viz. :—

Seedling of Wild Hop, Manitoba (2).

Hop of unknown origin × male raised from Golden Hop (1).

Seedling of 59a (American seedling) (1).

Seedling of late Bavarian hop (2).

Of one seedling (OV7) of the late Bavarian hop, only a few hills and strap-cuts have been attacked. In some seasons a number of rooted sets of this and other susceptible seedlings raised in the nursery have been killed by the fungus. The normal practice at the Research Station is for the rooted sets to be lifted from the nursery early in November and then bedded in until required for planting, which usually takes place during February. The sets

may appear to be quite healthy when lifted, but at planting time many are often found to be badly diseased or completely killed. This form of attack was serious only in the winters of 1927-8 and 1936-7, both of which followed wet summers very favourable for the spread of the disease.

In the earlier years the bine in the nursery beds was allowed to trail over the ground, but since 1933 it has been trained on low wirework (4 ft.) and has been sprayed regularly with Bordeaux mixture, hence infection in the rootstock was not so severe in 1936-7 as in 1927-8.

Whilst the majority of seedlings that have proved susceptible to infection of both strap-cuts and rootstock, have also shown themselves to be very susceptible to bine and cone infection, there have been certain exceptions. For example, M45 (Oregon Cluster × English male) has proved so susceptible to infection of the rootstock that it has been found impossible to keep the plot fully planted up, and those hills that do not become completely killed are so weakened that the yield per acre of the variety has been reduced by half since the advent of Downy Mildew. This seedling is not, however, particularly subject to the spike form of the disease, and has never been attacked on the cones, even when unsprayed. A few seedlings have borne badly diseased strap-cuts, although the hills have remained healthy. Of these, four are seedlings of a wild hop from Manitoba. Brewers' Gold (C9a), a seedling of this parentage, has suffered so severely from diseased strap-cuts in some seasons that propagation has had to be by means of runners. However, the rootstock has remained alive and has given rise to sufficient bine to produce an average crop over eight years of over 25 cwt. per acre.

Discussion.

Whilst the total amount of spike infection found in any year is largely determined by the seasonal weather conditions, the relative susceptibility of the various seedlings remains fairly constant, as is illustrated by the annual spike infection of Brewers' Favourite (OP21) and Early Promise (X35) shown in Fig. 1.

There are naturally some differences in susceptibility amongst seedlings of the same parentage, but seedlings of certain origins are notably more susceptible than others.

Most of the seedlings derived from late Bavarian, late German (260-1) and Elsass, together with all those of the New Mexican wild hop, are highly susceptible to attack on the bine, but the disease tends to give rise to rather different symptoms in the two groups. Seedlings derived from the first two German parents tend to have a large number of spikes per hill, and to

suffer from angular spotting of the lower leaves in years favourable to the fungus. The New Mexican seedlings have fewer spikes per hill, but have a definite tendency towards the production of lateral spikes on the lower half of the bine. Although so far only eight seedlings of the second generation from New Mexican Hop (seedlings of Y90) have been under trial, there is an indication that at least some of them will show less susceptibility than those of the first generation.

Whilst the great majority of the seedlings of the Manitoba wild hop are very subject to the spike form of the disease, a few are only moderately susceptible. The second generation of seedlings from Saaz and seedlings of Golden Hop range from very susceptible to moderately susceptible to bine infection, with a fairly uniform distribution.

The closest correlation between parentage and incidence of the disease occurs in seedlings derived from Oregon Cluster. All six seedlings of Oregon Cluster × English male have suffered severely from invasion of the rootstock by the fungus. This susceptibility has been passed on to the second and third generations via the seedlings M45 and M52 (seedlings of Oregon Cluster). Although many seedlings derived from M45 and OP13 (a seedling of M45) are liable to be killed by invasion of the rootstock, several seedlings show varying degrees of resistance to infection of the bine, even when attacked in the rootstock. Whilst seedlings of the second generation from Oregon Cluster, other than those of M45, are all very subject to the spike form of the disease, they are less liable to rootstock infection than those of M45 or OP13 (seedling of M45). Of twenty seedlings under trial only four have been attacked in the rootstock, and of these, three are derived from one particular Oregon seedling (M52), whereas nearly half the seedlings of M45 and OP13 have suffered from infection of the rootstock.

With the exception of certain seedlings derived from the New Mexican and Manitoba wild hops, all seedlings have produced cones free from disease when sprayed. It is therefore impossible to obtain an indication of the relative susceptibility of the majority of the seedlings to cone infection. It can, however, safely be assumed that those New Mexican and Manitoba seedlings which have been attacked on the cones even when sprayed, are highly susceptible to this form of the disease. Only two seedlings, L21 (Tolhurst × English male) and P43 (seedling of hop of unknown, English, origin) have shown marked resistance to the disease in all its forms. Unfortunately neither of these seedlings has proved of sufficient brewing value to warrant its introduction into commercial cultivation.

Under East Malling conditions, Fuggle has proved very resistant to the disease, but there are great differences between the several strains in the number of hills bearing spikes.

Six seedlings of various parentages have proved of sufficient brewing value and cropping capacity to warrant their introduction into commercial cultivation. They are the following:—

Brewers' Favourite (OP21)	= (Oregon Cluster × English male) × English male.
Brewers' Gold (C9a)	= Seedling of wild hop, Manitoba.
Quality Hop (OO63)	= 3rd Generation from Oregon Cluster.
Fillpocket (Z62)	= 2nd Generation from Oregon Cluster.
Cats-Tails (OZ79)	= Seedling of New Mexican hop.
Early Promise (X35)	= Seedling of hop of unknown origin.

The percentage of hills showing spikes in each season from 1931-6 inclusive for these seedlings is shown in Table III. Owing to changes in the hop garden

TABLE III.

Percentage incidence of hills with spikes of certain seedlings of proved merit, 1931-6.

Variety.	1931.	1932.	1933.	1934.	1935.	1936.
Brewers' Favourite (OP21)	81	100	81	25	6	75
Brewers' Gold (C9a) ..	87	93	80	60	13	47
Quality Hop (OO63) ..	73	67	44	nil.	nil.	100
Fillpocket (Z62) ..	38	90	—	—	nil.	13
Cats-Tails (OZ79) ..	81	94	69	19	nil.	94
Early Promise (X35)	93	93	93	40	nil.	47

which necessitated the grubbing and replanting of Fillpocket, no records of the incidence of spikes on this variety are available for the years 1933 and 1934. The incidence of the disease in 1936 was almost entirely confined to lateral spikes amongst the burr, and the figures for that year are not therefore strictly comparable with the others which are based on the normal basal and lateral spikes formed earlier in the seasons.

It will be seen that whilst there is considerable seasonal variation, all varieties have shown a high percentage of hills with spikes in a bad year such as 1932. However, there seems some indication that the Quality Hop is rather less subject to basal spikes than are the others, although it was severely attacked on the fruiting laterals in 1936.

The varieties in question have shown greater variation in their susceptibility to attacks on the cones. Brewers' Favourite has proved to be the most susceptible of the six varieties. It was severely attacked in 1927, when it was not sprayed, and slightly attacked in 1932 when it was sprayed twice. This variety makes a large amount of lateral growth rather late in the season, and therefore requires either heavier or more numerous applications of spray in wet seasons. The most recent recommendations of Salmon and Ware (7) are that four applications should be given to commercial varieties, so as to

ensure protection in years favourable to the spread of the disease. It is likely that, given this treatment, the cones of Brewers' Favourite would be completely protected.

Although the season in 1936 was very favourable to infection of the cones, a clean crop of Brewers' Favourite was obtained with only three applications on the whole half-acre plot, with the exception of four rows. Owing to a defect in the machine, these four rows did not receive a good covering of Bordeaux mixture at the first spraying. This shows the importance of the early application in seasons favouring the disease.

Brewers' Gold always makes a very large amount of lateral growth, nevertheless it has been possible to grow a clean and heavy crop with normal spraying. It was not in the gardens when they were not sprayed, but in 1931, a year favourable to cone infection, two applications resulted in a crop free from disease.

Quality Hop has been in the garden only since spraying has been practised, and it has never been attacked on the cones.

Fillpocket, also, has never been attacked on the cones, even in 1930, when it was not sprayed.

The New Mexican seedling, Cats-Tails, has shown itself less susceptible to attack than another heavy cropping variety of the same parentage which had a trace of infection in 1932 and 1933. Both varieties have been sprayed, except in 1930, when neither showed any infestion of the cones.

Early Promise must be considered definitely resistant to cone infection, as it was in the gardens before the advent of Downy Mildew, has been there ever since and has only once been attacked on the cones. This attack, which was only slight, was in 1927, a bad year for the disease, and the variety was unsprayed.

ACKNOWLEDGMENTS.

The writer is greatly indebted to Dr. G. H. Pethybridge for his help in preparing this paper for publication. Thanks are also due to Professor E. S. Salmon, of the South-Eastern Agricultural College, at whose suggestion the work of summarizing the several years' records was undertaken.

SUMMARY.

An account is given of observations on the incidence of Downy Mildew (*Pseudoperonospora Humuli*) from its first appearance in 1924 until 1936 on certain new seedling varieties of hops and on strains of Fuggle growing in the experimental garden at the East Malling Research Station, the main features of each season's outbreak being mentioned briefly.

The seasonal variation both in intensity and in the form of the disease (mainly spike production and cone infection) is shown to be largely influenced by the spring and summer rainfall.

The incidence of the disease on seedlings of various parentages is recorded, and it is shown that seedlings of certain crosses have, on the whole, had a high percentage of hills bearing spikes. Certain seedlings of *Humulus Americanus* and its variety *neo-mexicanus* have proved very susceptible to attack on the cones.

Some crosses have given rise to very susceptible seedlings and also to others which show some resistance to infection of the bine.

The closest correlation between parentage and susceptibility to the disease is shown by rootstock infection, practically all seedlings severely attacked in this way having originated from the same American variety. Only two seedlings so far tested have shown any very marked resistance to the disease. Of six new varieties recommended for commercial cultivation, some show a measure of resistance to attack either of the bine (or rootstock) or of the cones.

At East Malling, Fuggle has proved very resistant. The data obtained lend support to the view that there are various strains of this variety in cultivation.

Attacks of the disease on the cones have largely been prevented by routine spraying with Bordeaux mixture.

REFERENCES.

(1) *Salmon, E. S.* and *Ware, W. M.* The Value of Hop Breeding Experiments. Journ. Inst. of Brewing, 1917, **23**, 60-97.

(2) ———. The Downy Mildew of the Hop. Journ. Min. of Agric., 1925, **31**, 1144-51.

(3) ———. The Downy Mildew of the Hop in 1930. Journ. Inst. of Brewing, 1931, **37**, 24-31.

(4) ———. The Downy Mildew of the Hop in 1931. Journ. Inst. of Brewing, 1932, **38**, 37-44.

(5) ———. The Downy Mildew of the Hop in 1932. Journ. S.E. Agric. Coll., 1933, **32**, 108-119.

(6) ———. The Hop Downy Mildew and Its Control. S.E. Agric. Coll., Wye, 1931.

(7) ———. The Downy Mildew of the Hop in 1936. Journ. S.E. Agric. Coll., 1937, **40**, 37-43.

In addition to 2, 3, 4, 5 and 7 above, the general incidence of the disease year by year is given by Salmon and Ware in:—

(8) Journ. Min. Agric. (1925), **32**, 30-6; (1926), **33**, 149-61; (1927), **33**, 1108-21; (1928), **34**, 1093-99.

(9) Journ. Inst. of Brewing (1929), **35**, 20-5; (1930), **36**, 63-6; (1931), **37**, 24-31; (1932), **38**, 37-44.

(10) Journ. S.E. Agric. Coll. (1934), **34**, 107-118; (1935), **36**, 48-54; (1936), **38**, 48-52.

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TEMPERATURE—COLD INJURY CURVES OF FRUIT

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Part I.

GENERAL THERMOCHEMICAL CONSIDERATIONS.

Storage tests in South Africa have revealed a complex relation between the temperature of storage and the amount of physiological breakdown in various fruits. The results of these tests may briefly be summarized here, as a number of the original papers are still only in the course of publication.

Davies, Boyes, Beyers and De Villiers (10) observed that when samples of Japanese varieties of plums were stored at 31° F., 34° F., 37° F. and 40° F. for a period of twenty-five days, maximum internal breakdown occurred at 37° F. At 40° F. on the one hand and lower temperatures on the other there was less breakdown. Davies, Boyes and Beyers (9) later found that the maximum temperature at which breakdown of Japanese varieties of plums occurred was in the neighbourhood of 45° F. With lower temperatures breakdown generally reached a maximum at 37° F. and, with a storage period of twenty-five days, was reduced as the temperature fell below 37° F. These results have recently been confirmed by unpublished results of Davies and Boyes (5). The general result of all these experiments has been that breakdown usually reaches a maximum at an intermediate temperature around 37° F. and falls off either as the temperature is raised or lowered. An example is given in curve 1 of Fig. 1. Many other examples are given in the literature which has been cited. These results all refer to a relatively short storage period of about twenty-five days. With increasing periods of storage the position is gradually changed. This is a matter which will be discussed later—for the present only the results from relatively short periods of storage will be considered.

Pitting of the rind of Marsh grapefruit is similar. After three to four weeks storage pitting is rare both at temperatures as low as 30° F. to 32° F. or at temperatures as high as 50° F. to 55° F. In between these two extremes injury may be severe. This was first noticed in Florida (1) and, later, by Davies and Boyes (6). It has recently been confirmed with fruit from various parts of South Africa. A typical illustration is given in curve 2 of Fig. 2. This result, i.e. maximum pitting at an intermediate temperature, does not always hold for the more resistant, seeded varieties of grapefruit. These

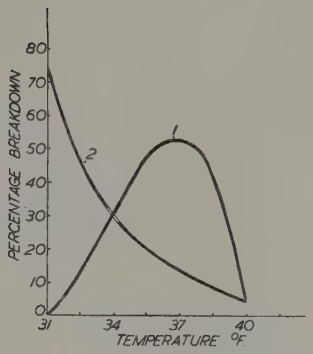

Fig. 1.

The effect of temperature of storage on breakdown of two samples of Santa Rosa plums. Intermediate ("B") stage of maturity. Storage period of 25 days. After Davies, Boyes and Beyers (9).

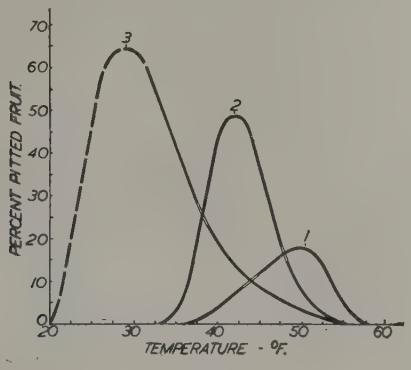

Fig. 2.

The effect of temperature of storage on pitting of Marsh grapefruit. Curve 1 from a very susceptible sample from the Western Province, stored for 14 days. Curve 2 from a sample from the Western Province stored for 23 days. Curve 3 from a fairly resistant sample from the Eastern Province stored for 67 days.

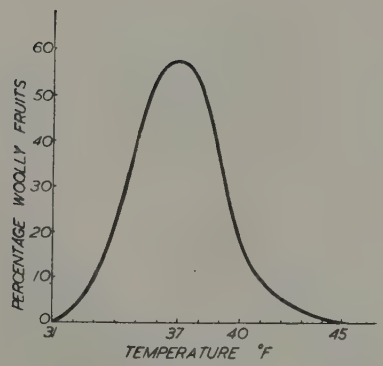

Fig. 3.

The effect of temperature of storage on woolliness of Peregrine peaches. Intermediate ("B") stage of maturity. Storage for 24 days. After Davies and Boyes (8).

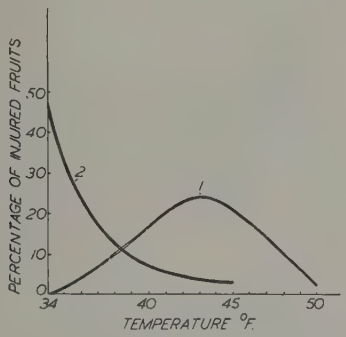

Fig. 4.

The effect of temperature of storage on injury to the rind of Navel oranges from the Western Province. Curve 1 from sample stored for 24 days. After van der Plank *et al* (18). Curve 2 from sample stored for 21 days. After Davies and Boyes (7).

varieties have generally been studied under conditions of prolonged storage for two or more months, a matter which is not being considered at this stage.

Woolliness of peaches behaves similarly. With a storage period of twenty-four days it is at a maximum at about 37° F. and is usually rare or absent either at 45° F. on the one side or 31° F. on the other (Davies and Boyes (8)). This is illustrated in Fig. 3.

Satisfactory relevant data for oranges are scarcer. Injury to the rind seems usually to increase regularly with decreasing temperature, giving the type of curve which has usually been accepted as a cold injury curve. This is shown by curve 2 of Fig. 4 which is taken from the results of Davies and Boyes (7). But on one occasion a peaked curve, similar to those already discussed, has been found. It is curve 1 of Fig. 4 which is constructed from the data of van der Plank, Rattray, Boyes and De Villiers (18).

The problem immediately arises whether these complaints which occur to a maximum extent at an intermediate temperature can be regarded as manifestation of cold injury. Whilst none of them occurs at high temperatures, yet all of them exhibit temperatures of maximum injury, below which injury decreases with decreasing temperatures. This would seem contrary to the generally accepted conception of cold injury. The objection appears superficial and unreal. It assumes that cold injury is due to a single factor, namely, the increasing maladjustment of the fruit to decreasing temperatures of storage. It ignores the fact that the actual visible manifestation of this maladjustment —i.e. the development of symptoms and lesions—involves processes within the fruit which are wholly or partly chemical in nature. The temperature relationships of cold injury are governed not only by the varying degrees of maladjustment of the fruit to varying temperatures, but also by the relationship between temperature and the rate of the chemical processes which finally render this maladjustment obvious. There are therefore at least two factors involved in a temperature-cold injury curve ; and it is with their interaction that this paper is concerned.

THE NECESSITY FOR A TEMPERATURE OF MAXIMUM INJURY.

A simple instance of cold injury is that of " tin pest ", i.e. the transformation in cold climates of the ordinary " white " form of elemental tin into the " grey " form which lacks the useful metallic properties which the element ordinarily possesses.* The change from one form into the other has been studied in some detail (see e.g. Mellor (14)). At temperatures above 18° C.—the transition temperature of one form into the other—white tin is stable, but

* The authors wish to thank Professor R. B. Denison for calling attention to " tin pest " as an example of cold injury.

below 18° C. grey tin forms at a rate which increases with a fall of temperature until −50° C. is reached. Below this temperature the rate of change reverses, and a further fall of temperature retards the transformation. There is thus a temperature of maximum rate of injury, corresponding with that found for breakdown of plums, woolliness of peaches and pitting of grapefruit. This is shown in Fig. 5.

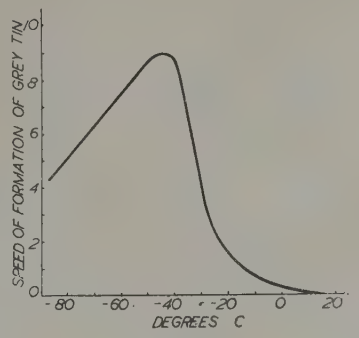

FIG. 5.

Relative speeds of transformation of ordinary tin to grey tin at different temperatures. After Mellor (14).

The two factors which appear to be responsible for this curve are:—

(1) *An equilibrium factor.* When the temperature of the metal is below the transition temperature, 18° C., the white form is out of equilibrium; and the degree of disequilibrium is related to the distance of the temperature from 18° C. There is probably no reversal in this process. The disequilibrium is probably always greater at a lower temperature; and for this reason the transformation of white tin may be regarded as an example of cold injury in its strictest sense.

(2) *A kinetic factor.* For the disequilibrium at low temperatures to become manifest, there must be a chemical change from white to grey tin. This change, like any other chemical process, is subject to the thermochemical rule that the rate of change is retarded by a fall in temperature. This rule thus introduces a factor which operates with respect to changing temperature in the opposite direction to the equilibrium factor.

Both factors operate at all temperatures below 18° C. but their effects are not always equally apparent. At temperatures just below 18° C. it is the effect of the equilibrium factor which is the more obvious; and if the temperature is brought up to 18° C. the transformation of white tin ceases because disequilibrium is eliminated. But at very low temperatures it is the effect of the kinetic factor which is the more obvious; and if the temperature is brought sufficiently low the transformation will cease, as all chemical changes can be made to cease by a sufficient reduction of temperature. In between these two extremes there is a point at which the opposite temperature effects of the two factors are just balanced. This is the temperature of maximum rate of injury.

Cold injury to fruit appears to be similar. What constitutes a healthy equilibrium—or, in more conventional terms, a healthy metabolism—is not

known. Nor is it known what type of disequilibrium is responsible for the symptoms of cold injury.* But, whatever it may be, it must involve chemical changes; and these changes must obey the rules of thermochemistry. The kinetic factor must therefore be admitted, and with it a temperature of maximum injury.†

Smith (15) has also suggested that two factors are present: a factor of "exposure" and one of "development".

THE SPECIAL CASE OF A PEAK BELOW FREEZING POINT.

The general thermochemical considerations show the necessity for a temperature of maximum injury, but they do not specify what this temperature will be. In practice it is found that the temperature varies. It varies with the susceptibility of the sample and with the period of storage. Even for a single variety of fruit widely different values may be found. An example of this is given in Fig. 2, in which the temperatures of maximum injury of three samples of Marsh grapefruit are shown to vary by as much as 20° F.

The reason for this will become apparent later. At this stage it is desired only to point out that, to conform with the thermochemical considerations, maximum injury may occur anywhere on the absolute scale of temperature. It may occur on either side of the freezing point.

In the examples of peaked curves which have been considered, the temperature of maximum injury has been above the F.P. of the fruit, and has therefore been within the range of experimental demonstration. But when maximum injury occurs below F.P., no experimental demonstration of its presence is possible, because the purely extraneous phenomenon of freezing arbitrarily limits the range of temperatures at which fruit may satisfactorily be stored. Freezing injury masks ordinary cold injury; and when the temperature of maximum injury falls below F.P. its presence can only be inferred.

An example of maximum injury below F.P. is given as curve 3 of Fig. 2. The continuous line was obtained experimentally for a rather resistant sample of Marsh grapefruit after relatively long storage. The broken line represents the expected continuation of this curve below F.P., which for grapefruit is in the region of 30° F. The whole curve shows a peak just below F.P. Curve 2

* It is possible that the disequilibrium results from the increased tendency towards exothermic reactions at the lower temperatures. This tendency must occur on thermodynamical grounds, particularly in those reactions, such as oxidation reactions, which involve a considerable exchange of heat. Even if one assumes that the tendency is not always followed by reactions *in vivo*, the tendency itself must be admitted. One must concede either that the tendency is followed as it would be by reactions *in vitro* or that the protoplasm, energized by respiration, must actively intervene to maintain the normal equilibrium. Either alternative would involve an abnormal metabolism which, at a sufficiently low temperature, might conceivably lead to injury.

† This argument in its simple form holds strictly only for what we shall term "primary susceptibility"; but with some modification of detail a similar two-factor hypothesis is applicable to "secondary susceptibility".

for plums in Fig. 1 is probably another example of a peak below F.P. This is unusual for Japanese varieties in South Africa. Similarly, curve 2 for oranges in Fig. 4 is probably another example.

On this basis the type of curve which shows a regular decrease of injury with increasing temperature and which, for this reason, has been considered as the normal type of cold injury curve is regarded simply as an incomplete fragment of a peaked curve extending below F.P. Curves with a peak and curves without an apparent peak are essentially similar, the only difference being that in the latter case injury is at a maximum below F.P. This is not a great difference since experience has shown that the position of the peak is labile and easily changed.

A lowering of the peak, with the resultant tendency to bring it below F.P., can occur for three separate reasons:—

(1) *A higher degree of resistance of the fruit.* It is evident that the greater the resistance of the fruit, the lower the temperatures which are necessary to cause injury. In other words, the greater the resistance, the greater is the tendency for cold injury curves to be situated farther down the temperature scale, with the consequent greater likelihood of a peak below F.P. (Quantitative evidence on this point is given later—Figs. 8 and 9.)

(2) *A longer period of storage.* As the period of storage is increased, so is the temperature of maximum injury decreased until it tends eventually to fall below F.P. This is discussed fully in Part II (see Fig 6 (a)).

A longer period of storage and a high degree of resistance are generally associated, for the reason that it is only with resistant types of fruit that long periods of storage are usually attempted. Since both long storage and great resistance tend to lower the temperature of maximum injury, it is to be expected that examples of incomplete curves with peaks below F.P. will be found more frequently with fruits which are relatively well adapted to cold storage. Conversely, high temperatures of maximum injury are likely to be found more often with those tropical and subtropical fruits which are easily injured by cold.

(3) *An increased rate of those chemical changes which render injury manifest as symptoms and lesions.* A faster rate of chemical change would have the same effect as a longer period of storage, in both cases the lowering of the temperature of maximum injury being due to a greater degree of progress in the chemical processes which render injury manifest.

A high rate of chemical change is partly responsible for the low temperature of maximum injury shown by the incomplete curve 2 of Fig. 1. The rate of manifestation of injury in this particular sample of plums was so fast that considerable injury occurred at 31° F. even after only twenty-five days. Usually with plums in South Africa, the rate is too slow for appreciable injury to occur in this time at 31° F.

A fast rate of chemical change in Marsh grapefruit seems to be associated with a high degree of maturity of the fruit or with prolonged delayed storage at high temperatures (van der Plank (17)).

Part II.

PRIMARY SUSCEPTIBILITY WHICH IS INHERENT IN THE FRUIT AT THE TIME OF STORAGE.

In Part I little attention was given to the effect of the length of the storage period. This has an important bearing on the question of cold injury curves and must be considered.

Fig. 6 shows the development of pitting in a sample of Marsh grapefruit from the Eastern Cape Province which was stored at six temperatures, 31·5° F., 35° F., 39° F., 45° F., 50° F. and 55° F. At 55° F. injury was negligible. At each of the other temperatures the behaviour is parallel. Injury begins after an interval of time and thereafter develops fairly rapidly. But it does not continue to develop until all fruits are affected, i.e. until 100% injury is recorded. Instead, it develops rapidly up to a point but beyond this it shows only a slight upward drift. These points are marked A, B, C, D and E on the 50° F., 45° F., 39° F., 35° F. and 31·5° F. curves respectively. For purposes of a first approximation, these points will be considered as true maxima throughout the whole of Part II of this paper. The slight upward drift beyond these points will be ignored for the present and discussed later (in Part III) as a separate phenomenon.

In another storage experiment, with Marsh grapefruit from the Eastern Transvaal, the absence of any great increase of pitting after the "maximum" had been reached was even more marked. Results are given in Tables I and II, Table I being for fruit in unwaxed sulphite wraps and Table II for fruit which had been wrapped at the packhouse in waxed crystalline paper. A part of the consignments was examined after five weeks and the rest after seven weeks. The Tables show no apparent increase of pitting during the interval, the small irregular change from five to seven weeks being well within the expected range of experimental error.

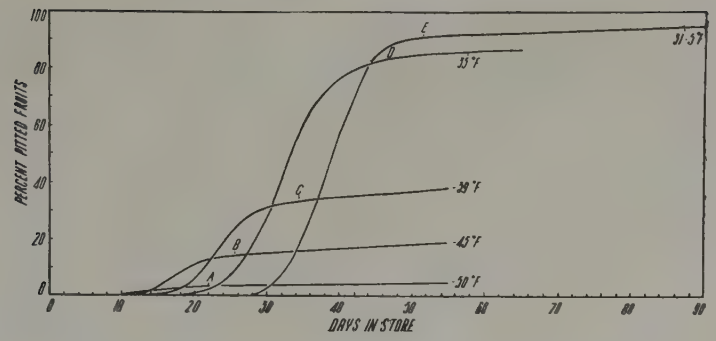

FIG. 6.

The effect of the period of storage on pitting of Marsh grapefruit at different temperatures. Sample from the Eastern Province.

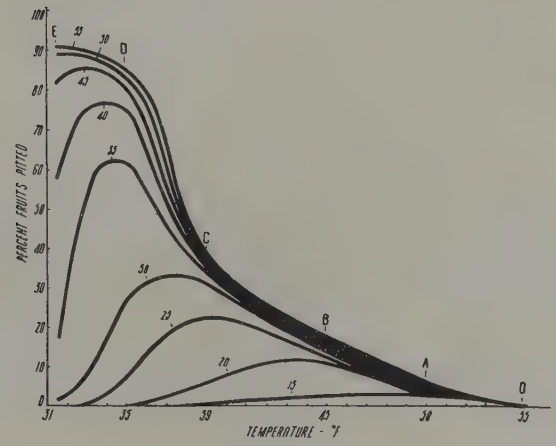

FIG. 6 (*a*).

The effect of temperature on pitting of Marsh grapefruit stored for varying periods. The curves are numbered to indicate the period of storage in days. From same data as for Fig. 6.

A similar observation has been made on Marsh grapefruit from South Africa by Tomkins and Dreyer (16). They found that although considerable pitting resulted from cold storage during shipment to England, there was no further increase if the fruit was re-stored after discharge. Similarly, Bates (2) has recorded that cold injury to oranges in Rhodesia develops during the first three or four weeks of storage at 36° F. and 40° F., and does not increase greatly with further storage. A curve showing a flattening after maximum

TABLE I.

The Percentage of Pitted Fruits in a Consignment of Marsh Grapefruit from the Eastern Transvaal. Fruit in Unwaxed Sulphite Wraps.

Storage Period (weeks).	Storage Temperature.			
	39° F.	45° F.	50° F.	55° F.
5	73·1%	50·0%	16·0%	0·9%
7	68·0%	52·2%	11·3%	0·8%
Increase	—5·1%	2·2%	—4·7%	—0·1%

TABLE II.

This Corresponds with Table I, except that the Fruit was wrapped at the Packhouse in Waxed Crystalline Paper.

Storage Period (weeks).	Storage Temperature.			
	39° F.	45° F.	50° F.	55° F.
5	52·3%	13·8%	4·2%	0·2%
7	58·0%	14·2%	1·9%	0·0%
Increase	5·7%	0·4%	—2·3%	—0·2%

injury was reached has also been found in one instance for Kelsey plums stored at 45° F. (Fig. 7). Lastly, Bělehrádek (3, p. 93) working on haemolysis by cold of ox erythrocytes in the presence of digitonine obtained curves very similar to those of Fig. 6. In this case the maximum was a true one, and there was an entire absence of any drift in haemolysis beyond the maximum with an increase of time.

In showing a "maximum", the curves in Fig. 6 differ strikingly from the sigmoid "mortality curves" usually obtained from fruit in store.

The development of a maximum seems to admit of only one reasonable interpretation: When a sample of fruit is stored at a constant temperature, a portion of the sample, depending on the susceptibility of the fruit, is out of equilibrium from the very instant of cooling, and is predestined to subsequent injury. The rest of the sample is in a state of healthy equilibrium as far as cold injury processes are concerned—it is in this state of healthy equilibrium from the moment of storage and continues in this state indefinitely. Time itself does not bring about the disequilibrium of the susceptible portion; the disequilibrium is inherent in the fruit from the beginning. Time is necessary

only to complete the chemical processes which result from the disequilibrium and which eventually result in visible symptoms and lesions.

A clearer idea of the issue is obtained if one adopts from chemistry the conception of a transition temperature—i.e. a temperature above which fruit will remain healthy and below which it will be injured. On this basis one may consider that portion of the fruit which is predestined to injury as having a transition temperature above the storage temperature, with the consequent inevitable tendency towards transition to the injured state. Conversely, that portion which remains healthy indefinitely may be regarded as possessing a transition temperature below the temperature of storage and being consequently out of danger.

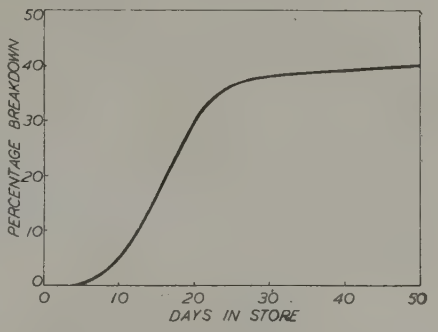

Fig. 7.

The effect of the period of storage on Kelsey plums stored at 45° F. After Davies, Boyes and Beyers (9).

Thus, to take a numerical example from Fig. 6, at 31·5° F. maximum injury was reached after about fifty-two days, at which time 90% of the fruits were injured. Further storage scarcely increased the proportion of injured fruits. The sample was thus made up of 90% of fruit with transition temperatures above 31·5° F. and 10% below; and, at 31·5° F., the time necessary for the completion of the chemical changes which make disequilibrium manifest was about fifty-two days.

The term "primary susceptibility" will be used for this type of susceptibility which exists at the time of cooling.

The Temperature Coefficient of Cold Injury Processes.

At present there is no known method by which one can follow the course of the chemical process, or chain of processes, which results from disequilibrium with the storage temperature. The mortality curve is simply an indication of the variability of the biological material: i.e. the difference between the times at which the fruits show injury is a measure of variation between individual fruits in the sample. The actual chemical changes which eventually result in visible injury of any particular fruit are not reflected in the mortality curve. Nevertheless, one can at least determine the time needed for the reactions to run to completion in the sample of fruit taken in the mass. This is the time

taken to reach maximum injury. From this knowledge one may determine the temperature coefficient of the process.

From Fig. 6 it is seen that maximum injury was reached in about fifty-two days at 31·5° F. (−0·3° C.) and in about twenty-five days at 45° F. (7·2° C.). Estimated from these figures, the value of Q_{10} within the range of the experiment is 2·7. In another experiment, also with Marsh grapefruit from the Eastern Cape Province, the corresponding times taken to reach maximum injury at 31·5° F. and 45° F. were fifty-one days and twenty-three days. Whence the estimate of Q_{10} is 2·9.

These estimates are not very accurate because of the difficulty of getting a precise reading from the curves. Nevertheless, their accuracy is sufficient to show that Q_{10} has a value which is common for ordinary chemical processes. The evidence thus accords fairly well with what has been said about the kinetic factor in Part I.

With stone fruits, which will be discussed later, the temperature relationships are usually more complicated.

THE DEVELOPMENT AND PROPERTIES OF A PRIMARY SUSCEPTIBILITY CURVE.

In Fig. 6 (a) are reproduced the same data as in Fig. 6, but they are now given in the form of a sequence of pitting-temperature curves at five-day intervals of storage, the curves being numbered to indicate the period of storage in days. The sequence begins in the region of the higher temperatures and gradually extends downwards to include the lower temperatures. In conformity with what has been said in Part I, the curves show a peak. At first this occurs at a high temperature. But with time it moves down to the lower temperatures until it eventually disappears beyond the range of the experiment, and the final curve is without a peak.

The sequence of curves in time builds up the curve O A B C D E from a temperature of 55° F. downwards. At 50° F. the point A, corresponding to point A in Fig. 6, is established after about twenty days; and, considering matters as a first approximation, further storage causes no increase of pitting. Similarly at 45° F. point B is laid down in about twenty-five days; at 39° F. point C in about thirty-five days; and so on, until the whole curve O A B C D E is complete after fifty to fifty-five days.

The curve must be treated as an approximation—in reality it is a series of curves running close to one another. This is because the points A to E on Fig. 6 are not exact maxima; the slight drift in pitting beyond the "maximum" results in a slight displacement with time of the curve in Fig. 6 (a). For present

purposes, however, this displacement will be ignored, just as the drift beyond the maximum in Fig. 6 has been ignored for purposes of approximation in Part II.

Considered in this way, the curve O A B C D E possesses a property which is unique among temperature-cold injury curves. When once sufficient time has elapsed for the curve to be formed, further time in store is without effect. The formation of the curve marks the elimination of the time element, and, with it, of the kinetic factor discussed in Part I.

By reading from the curves the amount of pitting corresponding to any temperature of storage, one obtains information on the primary susceptibility of the sample at any temperature. Thus, at 31·5° F., 35° F., 39° F., 45° F., 50° F. and 55° F., the corresponding percentages of pitting are, roughly, 90%, 85%, 35%, 17%, 5% and 0% respectively. About 90% of the fruit therefore had a transition temperature above 31·5° F.; 85% above 35° F.; 35% above 39° F.; 17% above 45° F.; 5% above 50° F.; and none above 55° F.

Since this curve gives all the necessary information about the primary susceptibility, it will be called the "primary susceptibility curve".

The properties of this curve are adequately defined if one knows (1) its shape and (2) its position relative to the temperature axis.

(1) *The shape of the curve.* This would seem to depend purely on the variability of the sample, i.e. on the difference in susceptibility between individual fruits in the sample. Curves which extend over a wide range of temperatures, as is usual with grapefruit, are indicative of great variability. It has, for example, already been pointed out that Fig. 6 (a) indicates that some fruits were so susceptible as to have a transition temperature above 50° F. while others in the same sample were so resistant that the transition temperature was below 31·5° F. Steep curves, on the other hand, indicate a large measure of homogeneity. With plums, for example, the curves are often so steep that a few degrees suffice to bring about a change from 0 to 100% injury. That is, the transition temperatures of the individual fruits of the population fall within a very narrow range.

It is unnecessary to discuss the subject in detail. Suffice it to say that by subdividing the temperature scale at small finite intervals and by measuring the increase in injury over each of these intervals, one may classify the fruits in the sample according to the interval of temperature at which transition occurs. In this way an ordinary frequency curve may be constructed to show the distribution of the transition temperatures of the fruits within the sample.

(2) *The position of the curve relative to the temperature axis.* It is evident that the position of the curve depends on the susceptibility of the fruit. The more susceptible the fruit, i.e. the higher the transition temperatures, the higher the curve will be situated along the temperature axis.

Experimental evidence indicates that the relation between susceptibility and position of the curve is very simple: Changing susceptibility is equivalent to the shifting of the whole curve, without modification of shape, up or down the temperature axis. This is shown in Fig. 8 which compares the pitting on Marsh grapefruit wrapped in unwaxed sulphite paper with that on fruit in waxed crystalline paper. The data are the same as those given in Tables I and II for a storage period of five weeks which, as shown by those Tables, is sufficient for maximum injury at all the temperatures concerned. In Fig. 8

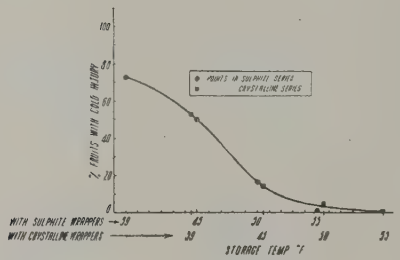

Fig. 8.

A comparison of the effects of waxed crystalline and sulphite wraps on pitting of Marsh grapefruit at different temperatures. The comparison is made by an alteration of the temperature axis. The storage period was 35 days.

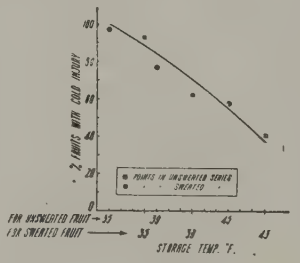

Fig. 9.

The effect of "sweating" for 6 days at 65° F. on the amount of pitting of Marsh grapefruit on subsequent storage for 45 days at different temperatures. The effect is shown in terms of a shift of the temperature axis.

the points for the crystalline-wrapped fruit are plotted against a temperature axis which is shifted 5.5° F. relative to the axis for fruit in plain sulphite paper. A single curve fits both sets of points. The effect of crystalline wraps in this experiment is thus seen to be equivalent to the raising of the storage temperature by 5.5° F. In other words, the increased resistance obtained by using crystalline wraps was equal to a reduction of 5.5° F. in the transition temperature of each fruit.

In Fig. 9 a similar comparison is made between "unsweated" Marsh grapefruit from the Western Province and fruit from the same source which had been "sweated" at a high humidity for six days at 65° F. The storage period was forty-five days, which was sufficient for maximum injury to be reached at all the temperatures concerned.

Two points must be observed with regard to the shifting of temperature-cold injury curves: Firstly, sufficient time in store must be given to allow the development of maximum injury, i.e. the curves must be fully-developed primary susceptibility curves. The results do not apply to the peaked curves

which are obtained with shorter periods in store. Secondly, the samples to be compared must be from the same source. They must be equally variable, i.e. the curves must be of the same shape, otherwise it is impossible to superimpose the one exactly on the other.

Part III.

SECONDARY SUSCEPTIBILITY, WHICH RESULTS FROM CHANGES IN THE FRUIT AFTER COOLING.

In Part II it has been considered that a maximum is reached, and that no further injury occurs after sufficient time has elapsed to bring about the injury of those fruits with a transition temperature above the storage temperature. This would be true if the transition temperatures existing at the time of cooling were fixed and unchangeable. Obviously, this is incorrect, although at times it may be sufficiently near the truth to serve as a good approximation. Fruit in store is not stable and immutable. It respires and continually ages* ; and as it ages, one may expect a change in the transition temperature, as one expects some changes in all properties of the fruit. If the tendency is for the transition temperature to rise, more fruit will be injured: and the gradual raising of the transition temperature will result in a gradual upward drift in the amount of injury.

Such susceptibility which is developed *after cooling* by the ageing and weakening of the fruit in store will be called " secondary susceptibility ". Its presence may logically be deduced from the upward drifting of injury with time, just as primary susceptibility may logically be inferred from the development of maximum injury beyond which there is no drift.

The amount of secondary susceptibility which may be developed varies considerably. In the grapefruit from the Eastern Transvaal considered in connection with Tables I and II, it seemed to be absent, or very nearly so. All the injury developed within the first five weeks of storage, and further storage did not weaken the fruit. The grapefruit from the Eastern Cape, considered in connection with Fig. 6, was not quite so free from secondary susceptibilty. As the fruit aged in store, it showed some weakening, which resulted in a gradual upward drift of the " mortality curve " beyond the points hitherto considered, for the purpose of approximation, as maxima. Nevertheless, the injury due to secondary susceptibility was small in comparison with

* Ageing, as referred to here, simply refers to the process of change with time in stored fruit. Up to the present there is insufficient evidence either to associate it with or to dissociate it from normal ripeness which occurs on the tree. For this reason the term " ageing " is used, because it is non-committal. It is hoped later to be able to compare or contrast " ageing " and normal ripening or senescence. But for the present, attention is being confined to the fact that there is an obvious ageing of fruit in store, without attempting to connect this ageing with any other process.

that due to primary susceptibility. But in all samples of Marsh grapefruit received from the Western Cape, the tendency towards secondary susceptibility was pronounced. The fruit weakened rapidly in store, with the result that the upward drift of the "mortality curve" was pronounced. Some examples will be considered later.

The reason for the presence or absence of a tendency towards secondary susceptibility is not yet known. (Some predisposing factors are at present under investigation.) It can be said at this stage merely that the factors which predispose a fruit to secondary susceptibility are not necessarily the same as those which cause primary susceptibility. This is illustrated by the sample of

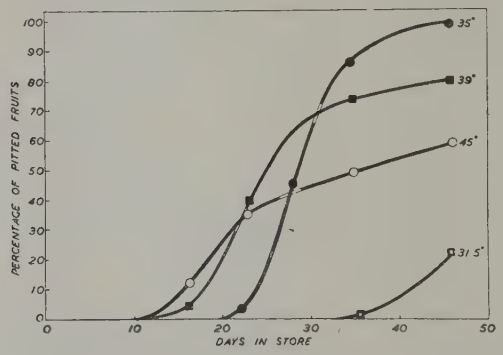

FIG. 10.

The effect of the period of storage on pitting of Marsh grapefruit at different temperatures. Sample from the Western Province.

grapefruit from the Eastern Transvaal which has already been discussed. In this sample the primary susceptibility was great. This is shown by the high percentages in Table I. Yet, coupled with this high primary susceptibility, there was a virtual absence of any tendency towards secondary susceptibility.

A few examples of pronounced secondary susceptibility will now be considered.

Fig. 10 shows the "mortality curves" obtained with a sample of fruit from the Western Province. Pronounced drifting is apparent at 39° F. and 45° F., and of the total pitting found after forty-five days a considerable proportion may be put down to secondary susceptibility.

Fig. 11 shows the "mortality curves" of another sample from the same orchard. With this sample the change from primary to secondary susceptibility is carried a step farther. Vestiges of the effects of primary susceptibility appear to exist in the "mortality curve" for 39° F., but at 45° F. no evidence of

primary susceptibility is apparent. At the time of cooling, the transition temperatures of the fruit were probably below 45° F.; and injury occurred only as the metabolic changes in store weakened the fruit and brought the transition temperature above 45° F.

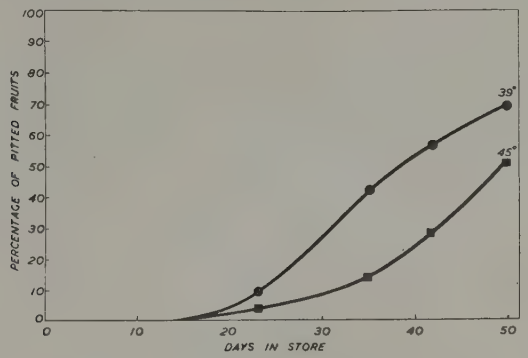

Fig. 11.

The effect of the period of storage on pitting of Marsh grapefruit at different temperatures. Sample from the Western Province.

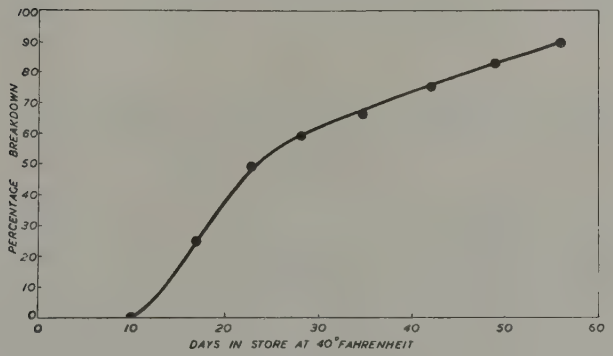

Fig. 12.

The effect of the period of storage on breakdown of Wickson plums at 40° F.

As far as one can judge from the data in the literature (4, 11), most of the results with the more resistant varieties of grapefruit—or with relatively resistant samples of Marsh—indicate a similar absence of any marked effect of primary susceptibility. Further work is needed on this point.

A pronounced tendency towards secondary susceptibility is shown in Fig. 12 for Wickson plums stored at 40° F. The curve is similar to the 45° F.

curve in Fig. 10. Plums from the same orchard showed almost 100% breakdown within twenty-five days at 37° F., which indicates that only a slight rise of transition temperatures is sufficient to cause secondary susceptibility at 40° F.

In one instance (Davies, Boyes and Beyers (9)—their Fig. 34) there is evidence of transition temperatures being raised above 50° F. with Wickson plums.

Apart from that given in Figs. 7 and 12, very little evidence on secondary susceptibility exists for stone fruits. As a general rule the primary transition temperatures of these fruits in South Africa fall within a narrow range, between about 40° F. and 45° F., the results in Figs. 7 and 12 being exceptions. It is therefore within this range that information on the balance between primary

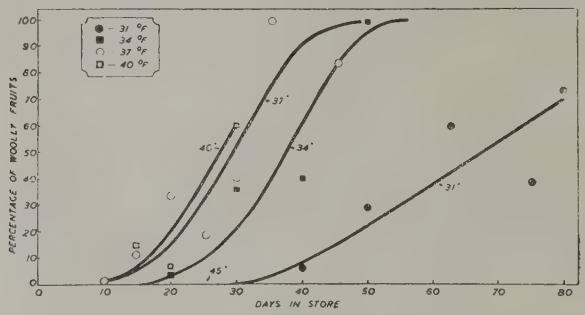

FIG. 13.

The effect of the period of storage on woolliness of Peregrine peaches stored at different temperatures. Fruit at 40° F. discarded for over-ripeness after 30 days. There was no woolliness at 45° F. After Davies and Boyes (8).

and secondary susceptibilty is likely to be collected. Unfortunately, temperatures within this range have scarcely been studied.

The type of curve usually found for stone fruits is shown in Fig. 13 for Peregrine peaches and Fig. 14 for Elberta peaches. Results with plums are usually fairly similar ; examples will be found in the literature already cited. In Figs. 13 and 14 the rapid rise of woolliness at temperatures of 40° F. or below indicate high primary susceptibility. Secondary susceptibility may also be involved, but this is difficult to determine from the data.

Although they have no direct bearing on the immediate problem under discussion, there are two points about Figs. 13 and 14 which may be mentioned in passing. Firstly, the rate of development of woolliness at 31° F. is very slow relative to that at the other temperatures. The temperature coefficient of the rate of manifestation of injury is itself a function of temperature, and increases markedly as very low temperatures are approached. In this respect peaches

differ from grapefruit, which has already been discussed. (For instances of the inconstancy of Q_{10} for biological process see, for example, Bělehrádek (3).) It is this fact which allows very low temperatures to be used occasionally to avoid injury. Unfortunately, this is not invariably true of stone fruits—Santa Rosa plums, for example, have shown great inconsistency on this point. Secondly, the rate of development of woolliness at all temperatures was greater in the sample of Elbertas than in the sample of Peregrines. Consequently, with a storage period of twenty-four days, woolliness in Elbertas could not be escaped by storing at 31° F., in spite of the fact that the Elbertas, like the Peregrines, showed a marked increase of the temperature coefficient at the lower ranges of temperature. Fortunately, Elbertas ripen comparatively slowly in

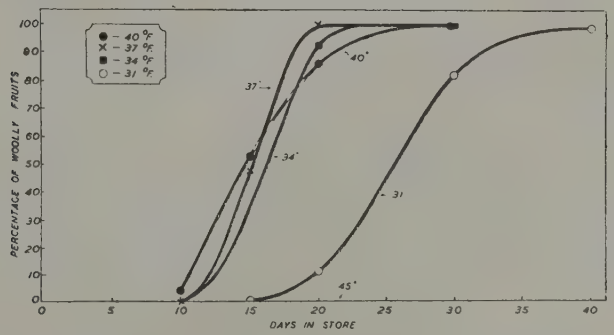

Fig. 14.

The effect of the period of storage on woolliness of Elberta peaches at different temperatures. Woolliness was absent at 45° F. After Davies and Boyes (8).

store, so it is probably feasible to avoid injury without incurring over-ripeness by shipping at temperatures above the woolliness range. With Peregrines, which ripen more quickly but develop injury more slowly than Elbertas, it would probably be more satisfactory to ship at temperatures below the woolliness range.

An Analysis of Cold Injury—Time Curves.

The primary susceptibility, existing at the time of storage, takes into account the factors which affect the susceptibility of fruit up to the time of cooling. The secondary susceptibility reflects the changes in the fruit after cooling. Between them, these two classes cover all possible sources of susceptibility, and form a complete scheme of classification. Moreover, each class leads to a different type of "mortality curve". From primary susceptibility it is logical to expect the development of maximum injury without further increase

with time ; while from secondary susceptibility a gradual increase of injury corresponding to gradual changes in the stored fruit is expected.* In this knowledge a satisfactory means of analysing cold injury curves is provided.

It is not intended to review the literature of cold injury curves in the light of this simple scheme of analysis. A single example will suffice to illustrate the amount of information which may be gained, for which purpose the data obtained by Kidd and West (12, 13) on cold injury of apples will be used, since they are comparatively extensive :—

At all storage temperatures, from −1·0° C. upwards, cold injury appeared after a long interval of time and increased steadily without any approach to a maximum. Such development of injury is typical of secondary susceptibility, and it is inferred that the transition temperatures at the time of storage were below the lowest storage temperature, i.e. below −1.0° C. Further, it was found that fruit which was cooled while passing through its respiratory climacteric was more susceptible than fruit in a pre- or post-climacteric phase. There can be alternative explanations of this result. The one explanation is that fruit which is cooled at the climacteric is more prone to those weakening changes in store which cause the transition temperature to rise—i.e. that such fruit bridges the gap between the initial transition temperatures and the storage temperature at a faster rate. Alternatively, one may assume that fruit at the climacteric has a greater primary susceptibility ; i.e. that the primary transition temperatures, although below −1·0° C., are higher than at the pre- or post-climacteric phase. In this case there would be a smaller gap to bridge by weakening changes between the initial transition temperatures and the storage temperature. The former alternative is the more probable. It was found that the difference between fruit cooled at the climacteric and other fruit was greater after forty-five weeks' storage than after thirty-nine weeks. This indicates that with fruit cooled at the climacteric there is that faster rise in transition temperatures which is required by the first alternative but not by the second. The weakness of fruit cooled at the climacteric thus seems to lie in the faster rate of change *after* cooling : the climacteric seems to affect secondary susceptibility, and there is, in these data, no direct evidence of any detrimental effect on primary susceptibility. It is possible that this faster rate of weakening is some relic of the fast rate of metabolic change which is normally associated with the climacteric at high temperatures. From this arises the question whether the rate of CO_2 production after cooling to very low temperatures is greatest for fruits that are cooled at the climacteric.

* Under certain circumstances a maximum might conceivably be reached even with secondary susceptibility. For example, the process of ageing might in some cases result in a decrease of susceptibility, i.e. in a lowering of transition temperatures. This would stop the upward drift of the curve. At this stage, however, it does not seem profitable to discuss such eventualities until they are actually found by experiment.

SUMMARY.

Part I.

After relatively short periods in cold store, breakdown of plums, woolliness of peaches and pitting of Marsh grapefruit usually occur to a maximum extent at intermediate temperatures. At higher or lower temperatures there is less injury. That is, the injury temperature curves usually show a peak.

This peak seems to be a necessary consequence of the interaction of two opposing factors in the development of cold injury:—

(1) *An equilibrium factor.* Lowering the temperature increases the disposition towards injury.

(2) *A kinetic factor.* The higher the temperature the sooner does the injury become manifest, indicating a process governed by the thermochemical rule that the rate of change is reduced as temperature is lowered.

The temperature of maximum injury is labile and is not a fixed characteristic of the fruit. It may occur above or below the freezing point of the fruit. The latter cannot be demonstrated but must be assumed. The gradation from a peaked curve to an incomplete curve without demonstrable peak has been shown for Marsh grapefruit.

The three factors which lower the temperature of maximum injury are:—

(a) greater resistance of the fruit;

(b) longer period of storage;

(c) a faster rate of manifestation of injury.

Part II.

The number of fruits injured does not increase indefinitely as the period of storage is lengthened. A "maximum" is reached which is sufficiently definite to be considered as a first approximation.

The number of fruits injured when the maximum is reached is greatest at the lowest temperature, but the maximum is reached soonest at the highest temperature. Q_{10} values are given for the rate of development of injury.

The fact that a maximum is reached at each storage temperature indicates that the susceptibility to injury exists in the fruit at the time of cooling. This is referred to as "primary susceptibility".

Frequency distribution curves of the "primary susceptibility" of a population of fruit over a range of storage temperatures can be prepared.

It is shown that the efficacy of any measure which reduces primary susceptibility may be measured in terms of shifting the frequency distribution curves of susceptibility down the temperature axis.

PART III.

The maximum injury referred to in Part II is not always a true maximum. Fruit changes during storage, and these changes result in further development of susceptibility to injury. This is referred to as "secondary susceptibility".

Injury due to primary and secondary susceptibility can be allocated. Various fruits may show only primary or secondary or both together.

The factors which predispose fruit to secondary susceptibility do not appear to be directly related to those causing primary susceptibility.

The simple scheme of analysis proposed is applied to the data of Kidd and West on cold injury of apples to illustrate the amount of information which may be gained.

LITERATURE CITED.

(1) *Anonymous.* Refrigeration Studies. Univ. of Fla. Agri. Expt. Sta., 45th Ann. Rpt., pp. 88-9, 1931.

(2) *Bates, G. R.* Storage Tests with Rhodesian Oranges during 1934. British South African Co., Mazoe Expt. Sta., Publ. No. 4, pp. 107-33, 1936.

(3) *Bělehrádek, J.* Temperature and Living Matter. Protoplasma Monographien, Vol. 8, 277 pp., Berlin, 1935.

(4) *Brooks, C.* and *McColloch, L. P.* Some Storage Diseases of Grapefruit. Journ. Agri. Res., Vol. 52, pp. 319-52, 1936.

(5) *Davies, R.* and *Boyes, W. W.* Cold Storage of Plums. Low Temp. Res. Lab., Capetown, Ann. Rpts. 1935-36 and 1936-37 (to be published).

(6) ———. The Effect of Temperature of Storage, Wilting and Delayed Storage on Pitting of Grapefruit. Low Temp. Res. Lab., Capetown, Ann. Rpt. 1934-35, pp. 161-3, 1936.

(7) ———. The Effect of Wilting and of Temperature of Storage on Cold Injury of Navel Oranges. Ibid, pp. 163-5.

(8) ———. Cold Storage of Peaches. Low Temp. Res. Lab., Capetown, Ann. Rpt. 1936-37 (to be published).

(9) *Davies, R., Boyes, W. W.* and *Beyers, E.* Cold Storage of Plums. Low Temp. Res. Lab., Capetown, Ann. Rpt. 1934-35, pp. 78-114, 1936.

(10) *Davies, R., Boyes, W. W., Beyers, E.* and *De Villiers, D. J. R.* Cold Storage of Plums. Low Temp. Res. Lab., Capetown, Ann. Rpt. 1933-34, pp. 66-84, 1935.

(11) *Friend, W. H.* and *Bach, W. J.* Storage Experiments with Texas Citrus Fruit. Texas Agri. Expt. Sta., Bull. 446, 40 pp., 1932.

(12) *Kidd, F.* and *West, C.* The Cause of Low Temperature Breakdown in Apples. Dept. Sci. Indust. Res., Food Invest. Board, Rpt. for 1933, pp. 57-60, 1934.

(13) ———. Temperature and Duration of Life in Apples. Dept. Sci. Indust. Res., F.I.B. Rpt. for 1935, pp. 97-101, 1936.

(14) *Mellor, J. W.* A Comprehensive Treatise on Inorganic and Theoretical Chemistry, Vol. 7, p. 301, London, 1927.

(15) *Smith, A. J. M.* The Precooling of Fruits in South Africa. Rept. to Union of S. Africa, Dept. Agri. and Forestry, p. 56, 1937.

(16) *Tomkins, R. G.* and *Dreyer, D. J.* A Note of Low Temperature Breakdown of Grapefruit from Somerset West. Farming in S. Africa, 12, pp. 157-8, 1937.

(17) *van der Plank, J. E.* Delayed Storage of Marsh Grapefruit. Low Temp. Res. Lab., Capetown, Ann. Rpt. for 1936-37 (to be published).

(18) *van der Plank, J. E., Rattray, J. M., Boyes, W. W.* and *De Villiers, D. J. R.* The Effect of Temperature of Storage on Navel Oranges. Low Temp. Res. Lab., Capetown, Ann. Rpt. for 1936-37 (to be published).

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A NOTE ON THE USE OF α-NAPHTHALENE ACETIC ACID FOR ROOTING SOFT-WOOD CUTTINGS OF FRUIT TREE STOCKS

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CONSIDERABLE evidence has now accumulated from various parts of the world, including this country (Tincker (1)), to show that the synthetic growth substances introduced by the workers at the Boyce Thompson Institute, Hitchcock and Zimmerman (2), Van der Lek and Krijthe (3), are of considerable value in propagating plants from cuttings. Two main methods are commonly used for applying growth substances. Either a lanolin paste containing the substance is smeared on the cuttings or they are immersed in an aqueous solution for a short time before planting. Hitchcock and Zimmerman (2) have shown the second method to be much the more effective. In the present tests only this method was used. Experiments with cuttings of *Lonicera nitida* and *Prunus Cerasifera* var., Myrobolan B, using indoleacetic, indolebutyric and naphthalene acetic acids, indicated that α-naphthalene acetic acid is the most active compound of the three for promoting root formation. Hitchcock and Zimmerman (4), in a recent publication, have also shown that this substance is more effective than other synthetic growth substances for rooting cuttings, and in addition they state that salts of the acid are equally effective and less likely to prove toxic (to plant material) at high concentrations.

Work has therefore been begun at East Malling to determine whether the growth substances are also effective for fruit tree cuttings. Before starting large scale experiments in the open or in unheated frames, preliminary tests are being carried out in propagating frames with bottom heat. Here a considerable range of concentrations and times of treatment are being tried on soft-wood cuttings of a number of varieties of fruit tree rootstocks. Several different growth substances are being used. The object is to determine the best range of concentrations and periods of treatment, the most promising substances and suitable material to use in large scale experiments.

This note describes some of the results so far obtained with α-naphthalene acetic acid.

This acid is not readily soluble in water, so the solutions were prepared by dissolving it in 1-2 cc. of 95% alcohol, and making it up to the required volume with tap water. The treatment of the cuttings was simple. They were freshly made, their lower leaves being removed as it was found that these tend to rot if they come into contact with the solution. The basal inch of the cuttings was immersed in the solutions which were freshly prepared for each experiment. When testing a given species of cutting, solutions containing from 10 p.p.m. to 50 p.p.m. were generally used. After the period of immersion, which was usually from 6-18 hours, the bases were carefully rinsed in tap water, and the cuttings planted in Bedfordshire sand in a frame with bottom heat.

Prunus Cerasifera Selection: Myrobolan B (Plum Rootstock).

This variety is a fairly ready-rooting subject from hardwood cuttings. The trees from which the cuttings were taken had been potted up in the winter and placed in a heated greenhouse. The tips of terminal shoots in active growth were used as cuttings on April 24th and subjected in groups of five to various treatments. Four weeks later they were examined for rooting and it was found that a solution containing 30 p.p.m. α-naphthalene acetic acid with immersion of the bases for twelve hours had been most effective, all five cuttings being well rooted. Only one of the controls, all of which had been treated for a similar time with water, had one small root. On the treated series the roots arose not only from the end of the cutting but also from the stem above. (See Fig. 1.)

Pyrus communis "Free" Pear Rootstock Selections.

(a) Malling C.8.

From indoor material. Actively growing shoots were taken from potted material growing in a heated greenhouse, and were treated with various concentrations of α-naphthalene acetic acid in batches of five on April 24th. A solution containing 40 p.p.m. with immersion for twelve hours was very effective, all five cuttings rooting after five weeks, whilst in the untreated batch none had rooted (Fig. 2).

From outdoor layer beds. In view of the promising results obtained with pear cuttings taken from specially prepared material, cuttings taken from material growing in the open were tried.

Lateral shoots on which the terminal bud had just stopped growth were taken from current season's growth on layer beds on June 17th and treated with various concentrations of α-naphthalene acetic acid. There were twenty cuttings in each treatment. A solution containing 40 p.p.m. α-naphthalene acetic acid with immersion for twelve hours gave the best result. Fifteen of the cuttings were well rooted after four weeks, whilst the remaining five were just starting to root. The untreated control cuttings had callussed but none had rooted.

(b) Malling C.2. (*From a tree growing in the open.*)

Lateral shoots which had just stopped growing were taken from a twelve year old tree on May 26th, and subjected to various treatments in batches of ten. Treatment with a solution of α-naphthalene acetic acid containing 30 p.p.m. and an immersion time of twelve hours caused five out of ten cuttings to root after five weeks, whilst none of the untreated controls had rooted.

Other Fruit Tree Cuttings.

Other species were also similarly treated: With black currants (*Ribes nigrum*), which normally root readily from both hard and soft-wood cuttings, it was found that there was a marked acceleration in the time of rooting. Fig (*Ficus Carica*) cuttings, taken from a tree growing in the open, had rooted after two weeks, whilst the controls callussed but formed no roots during the same period.

The preliminary results described in this note show that treatment with α-naphthalene acetic acid, which proved the most effective of three growth substances tested, greatly stimulated rooting of certain fruit tree cuttings. The optimum strength of the solution ranged from 30-40 p.p.m., according to the species, when the time of immersion was about twelve hours.

The rooting of soft-wood cuttings of the Malling pear stocks, taken from material growing outdoors, is a very promising result, as these are acknowledged to be very difficult material from which to propagate vegetatively (5). These results were obtained with small numbers of cuttings and the use of bottom heat. It is intended to carry out further tests with larger numbers of cuttings to determine whether rooting can be induced and accelerated after suitable treatment when they are planted in the first instance in a cool frame in the open.

SUMMARY.

Preliminary tests on small numbers of soft-wood cuttings of certain plum and pear rootstocks and of black currant and fig indicate that immersion of the bases for twelve hours in 30-40 p.p.m. α-naphthalene acetic acid improved rooting markedly.

LITERATURE CITED.

(1) *Tincker, M. A. H.* Experiments with Growth Substances, or Hormones, and the Rooting of Cuttings. Journ. Roy. Hort. Soc., 61, 510. 1936.

(2) *Hitchcock, A. E.* and *Zimmerman, P. W.* Effect of Growth Substances on the Rooting Response of Cuttings. Contrib. Boyce Thompson Inst. 8, 63. 1936.

FIG. 1.

Rooting of soft-wood cuttings of Myrobolan B. plum rootstock after four weeks. Upper row, untreated. Lower row, treated with a solution of α-naphthalene acetic acid, 30 p.p.m., for 12 hours.

FIG. 2.

Rooting of soft-wood cuttings of Malling Pear stock C.8, after five weeks. Upper row, untreated. Lower row, treated with a solution of α-naphthalene acetic acid, 40 p.p.m., for 12 hours.

(3) *Van der Lek, H. A. A.* and *Krijthe, E.* Bevordering van de wortelvorming van stekken door middel van groeistoffen, with a summary: Stimulation of cuttings by growth substances. Mededeelingen van de Landbouwhoogeschool, Wageningen, 41. 1937.

(4) *Zimmerman, P. W.* and *Hitchcock, A. E.* Comparative effectiveness of acids, esters and salts as growth substances and methods of evaluating them. Contrib. Boyce Thompson Inst., 8, 337. 1937.

(5) *Bagenal, N. B., Garner, R. J.* and *Hatton, R. G.* A Practical Evaluation of Rootstocks in Commercial Circulation. East Malling Ann. Rpt. (1936), 281. 1937.

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THE JONES-BATEMAN CUP FOR RESEARCH IN FRUIT CULTURE

In 1920 Miss L. Jones-Bateman, of Cae Glas, Abergele, presented to the Royal Horticultural Society a valuable silver-gilt replica of the Warwick Vase to be used for the encouragement of fruit production. It was accordingly decided to offer it triennially for original research in Fruit Culture which has added to our knowledge of cultivation, genetics, or other relative matters, and it is available for award in 1937.

Candidates should submit accounts of their work by October 30th. The work dealt with should have been mainly carried out by the candidate in the United Kingdom, and mostly during the preceding five years. The cup will be held for three years by the successful candidate, who must give a bond for its safe return. The holder will be eligible to compete on the next or any succeeding occasion. When the cup is relinquished the holder will receive a Hogg Medal specially struck in gold.

The Assessors will be three, two appointed by the Royal Horticultural Society and one by the National Farmers' Union, who will report to the Council of the Royal Horticultural Society upon the originality and comparative potential value to the fruit-growing industry of the work of the candidates.

The Council of the Royal Horticultural Society will award or withhold the cup at its discretion.